Is *Fuchsia excorticata* (Onagraceae) seed limited?

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Table of Contents

List of Tables

List of Figures

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Abstract

Maintenance of native bird populations is necessary for the effective functioning of bird-plant mutualisms such as pollination and dispersal. The New Zealand native tree *Fuchsia excorticata* (Onagraceae) is declining because of possum herbivory, and is known to be pollination limited resulting in lower seed set. However, pollination limitation will not be of any consequence if *F. excorticata* is not seed limited. I tested whether *F. excorticata* is seed limited. If the species is both pollen and seed limited, it has considerable implications for one of New Zealand's important secondary succession forest trees, as well as the honeyeating and frugivorous birds that feed on its flowers and fruit.

To compare whether local bird density and the pollination service affected the seed supply, I selected two sites with high pest control, and two sites with low pest control. Visitation rates to *F. excorticata* flowers and bird counts were measured at each site. I measured the seed bank at increasing distance from parent *F. excorticata* trees, and recorded the sex of parents to determine if pollination limitation was affecting seed set according to parent gender because females are more pollen limited than hermaphrodites. A field seed addition experiment tested for seed, microsite and herbivore limitation. Natural seedling distribution was mapped to distinguish what environmental conditions favoured germination and establishment.

Surprisingly, bird visitation to *F. excorticata* was no higher with pest control, but abundance of honeyeating birds was higher in five minute bird counts. The *F. excorticata* seed bank decreased with dispersal distance away from the parent tree, was larger in sites with high pest control and also significantly more abundant beneath hermaphrodite parents. On average seven times more seedlings germinated in sown plots than unsown plots, thus proving seed limitation. Caged plots had nearly twice as many seedlings as uncaged plots, which shows herbivore limitation. More seedlings germinated closer to the parent tree than further away. Therefore, *F. excorticata* is showing evidence of seed, microsite and herbivore limitation, and complex interactions between each. Most importantly, the pollination limitation that *F. excorticata* experiences due to lack of suitable pollinators causes a reduced seed set which affects the soil seed bank and level of seedling regeneration. This reduced seed

supply combined with seed and microsite limitation is affecting the density of *F. excorticata* seedlings, and thus perhaps ultimately the density of adult trees.

CHAPTER 1: INTRODUCTION

'What escapes the eye, however, is a much more insidious kind of extinction: the extinction of ecological interactions' – Janzen 1974

1.1 Bird-plant mutualisms

1.1.1 Overview

Global extinction and reduction in density of bird species has led to concern regarding possible subsequent losses of plant species, the loss of agricultural pest control, spread of disease, and reduced efficiency of ecological interactions such as flower pollination and fruit dispersal (Sekercioglu *et al*. 2004). This is of particular concern in New Zealand where sixteen bird species have become extinct since 1840, and 153 are threatened (including subspecies) (Hitchmough *et al*. 2005), threatening pollination and dispersal services (Clout and Hay 1989, Newstrom and Robertson 2005, Kelly *et al*. 2010).

Drivers of global environmental change such as land use change and biotic invasions can cause pervasive impacts on antagonistic and mutualistic interactions (Aizen *et al*. 2008, Tylianakis *et al*. 2008). Some flower visitors are sensitive to changes in habitat quality and/or quantity, which disrupts the efficiency of plant-pollinator interactions (Aizen *et al*. 2002), and ultimately the functionality of some mutualisms. These complex biotic interactions help to maintain biodiversity (Bascompte *et al*. 2006), so the disruption of these processes can cause further negative consequences for species in their habitat.

Maintenance of native bird populations is essential to the continued functioning of most bird-plant mutualisms (Kelly *et al*. 2010). Bird density reductions through loss of habitat and resources may lead to declining abundance of their dependent mutualist plant species, which is perturbing in New Zealand as the proportion of bird-pollinated plants is relatively high compared to the rest of the world (Sekercioglu *et al*. 2004).

Birds that are endangered, critically endangered or extinct in the wild are defined as “functionally extinct” (Sekercioglu *et al*. 2004). Bird species that have undergone recent and substantial declines in abundance and/or the extent or occupancy of their geographic

range (and possible function) are defined as “functionally deficient”. By 2100, 7 – 25% of birds are expected to be functionally extinct, and 13 – 52% are likely to be functionally deficient (Sekercioglu *et al*. 2004), with some guilds (including frugivores and nectarivores) likely to have greater than average extinction rates given the current magnitude of climate change, habitat loss and biotic invasions. There is an urgent need to perform long term, experimental and community based research that compares the efficiency of intact and reduced bird populations (Sekercioglu 2006).

The probability of pollinator or dispersal failure, the reproductive dependence on the mutualism and the demographic dependence on seeds can be used to predict the risk of plant declines (Bond 1994). Plants may compensate for high risk in one of these categories by low risk in others. For example, a plant may reproduce vegetatively, may self pollinate if insect pollinators are not active in inclement weather conditions, or flowers could be generalist, where they are able to be pollinated by birds or insects. Breeding system can also help determine reliance on pollination for seed set (and therefore reproductive dependence on pollinators) (Bond 1994).

1.1.2 Dispersal versus Pollination

Early mutualism research in New Zealand concentrated on dispersal services (McEwen 1978, Godley 1979, and Clout and Hay 1989). This focus stemmed from the fact that several large fruited plants “depend almost entirely on kereru for their dispersal” (Clout and Hay 1989, p32). The kereru (*Hemiphaga novaeseelandiae*) is the only bird that has a gape large enough to swallow the biggest New Zealand fruit. Eleven species have fruit greater than 10 mm diameter (specifically 5 species with fruits greater than 14 mm diameter: tawa *Beilschmeidia tawa*, taraire *Beilschmeidia tarairi*, karaka *Corynocarpus laevitagus*, tawapou *Planchonella costata*, and puriri *Vitex lucens*) (Clout and Hay 1989). Other frugivorous bird species exist that have gapes larger than 10mm but are functionally extinct because of their reduced distribution, (for example kokako *Callaeas cinerea*). Of the above large seeded trees, (except for taraire), seeds are produced that are small enough for the tui (*Prosthemadera novaeseelandiae*, Meliphagidae), to swallow and disperse with a large individual gape size disproving Clout and Hay’s (1989) dependence on kereru (Kelly *et al*. 2010).

be inefficient because of a size mismatch, where they do not contact the stigma, or they can only access the nectar by robbing at the base of the flower (Kelly *et al*. 2010). Anderson (2003) collected data on two ornithophilous species (*Sophora microphylla* and *Metrosideros excelsa*), and three entomophilous (insect pollinated) species (*Pittosporum crassifolium, Geniostoma ligustrifolium* (now *G. rupestre*) and *Pseudopanax arboreus*) for pollination limitation by excluding birds with wire cages. She found that fruit set was significantly reduced in all five species, regardless of open access of insects. This shows the importance of birds to typically insect pollinated species as well bird pollinated species (Anderson 2003).

1.2 Pollination limitation and crises

1.2.1 Overview

Pollination limitation is the decline in potential seed set following inadequate pollen delivery (Larson and Barrett 2000, Aizen *et al*. 2002, Ashman *et al*. 2004). Any reduction in pollinator service can cause seed numbers and quality to diminish, thus threatening the plant population viability, and ultimately the demographic collapse of the population (Aizen *et al*. 2002, Ashman *et al*. 2004). It is therefore essential to determine the strength of the mutualist service to establish the risk of plant population declines (Kelly *et al*. 2004).

Within a population, ecological context, plant life history, mating system and phylogenetic history can all affect the likelihood and strength of pollination limitation (Ashman *et al*. 2004). At the community level, understanding the importance of pollination limitation in plant diversity maintenance is vital to establishing the ecological and evolutionary outcomes of the phenomenon (Ashman *et al*. 2004). Ultimately, knowledge about whether plants can evolve to ameliorate the effects of pollination limitation, and how the population dynamics are affected are essential to understanding plant communities.

Conservation management strategies that focus on improving species habitat, rather than simply their abundance, could be the necessary approach for improving mutualist

Since these influential papers that focussed on the dispersal paradigm, much research has shown the importance of pollination services, which are now considered more susceptible to failure than dispersal of seeds (Kelly *et al*. 2004, Kelly *et al*. 2010). Germination of 18 of New Zealand's fleshy fruited species (including those with large fruits greater than 8 mm) is possible even if it has not passed through a bird gut (Robertson *et al*. 2006, Kelly *et al*. 2010). On offshore islands where there are few predators and high numbers of birds, avian pollinators are frequently observed visiting entomophilous (insect pollinated) flowers, and are able to gain enough energy rewards from these visits (Castro and Robertson 1997).

Most visits to native flowers in New Zealand are performed by only three native bird species that have brush tongues typical of honeyeaters: bellbird *Anthornis melanura* (Meliphagidae) (32%), silvereye *Zosterops lateralis* (Zosteropidae) (31%) and tui (25%) (Kelly *et al*. 2010). However it is likely that kaka *Nestor meridionalis* (Psittacidae), stitchbird *Notiomystis cincta* (Meliphagidae) and kokako were also important when their populations were more prolific than present day numbers (Kelly *et al*. 2010). This is indicated by the fact that stitchbirds performed 15% of pollination visits on the predator free sanctuaries where they still occur (Tiritiri Matangi and Little Barrier Islands) (Kelly *et al*. 2006).

Pollen and seeds have quite different "targets" (Howe and Westley 1988). Pollen can often fail because it does not reach its target (a receptive stigma of the same species), whereas seeds can often fail after they reach a potentially suitable target (an establishment microsite). There are myriad adaptations of flower form and function of plants that aim to achieve maximum pollination efficiency (Howe and Westley 1988). For example, *Delphinium nelsonii* and *Ipomosis aggregata* flower consecutively, are both pollinated by hummingbirds, and suffer reduced seed set during the brief period when the flowering overlaps. Waser (1978) suggests their distinct flowering periods are maintained by competition for pollination mutualist partners.

Birds were largely unknown as pollinators in Britain and Europe, which led to insects traditionally being seen as the primary pollinators in New Zealand (Thomson 1927). Insects were originally considered suitable alternative pollinators of ornithophilous (bird pollinated) flowers (Godley 1979; Clout and Hay 1989), but they are now known to often

services such as pollination (McAlpine and Wotton 2009). For example, stoat control led to increased bellbird nesting success in Kelly *et al*. (2005), but unfortunately did not show significantly improved mistletoe pollination. This approach to conservation looks at a broader picture of ecosystem function, not purely numbers of species.

1.2.2 New Zealand Pollination limited species

New Zealand ornithophilous flowers now show evidence for widespread pollination limitation (Kelly *et al*. 2010). There are 29 ornithophilous plant species in New Zealand, of which 8 out of 10 that were tested were found to have seed production reduced by at least one third due to reductions in pollination services (according to the Pollination Limitation Index (PLI), Larson and Barrett 2000). In two severe cases of pollination limitation, more than two thirds of the potential fruit set was lost. Pollen limitation is extensive on the New Zealand mainland, with higher than average pollination limitation indices than the global average (Kelly *et al*. 2010).

Theoretically, self-incompatible species should be more severely pollen limited than self-compatible species (Kelly *et al*. 2010). However, some of the most highly pollen limited New Zealand species are self-compatible (*Peraxilla tetrapetala, Rhabdothamnus solandri, Fuchsia perscandens*), although not autonomous selfers (Newstrom and Robertson 2005).

The failure of development of ovules into fruit may be because of insufficient quality and quantity of pollen (pollen limitation), not enough resources to convert ovules into seeds (resource limitation) or the occurrence of pathogens or herbivores in seed development (herbivore limitation) (Delph 1986, Schemske & Horvitz 1988, Larson & Barrett 2000). For instance, the New Zealand shrub species *Fuchsia perscandens* has fruit set 1.7-2.7 times higher in hand pollinated flowers than in non-manipulated flowers (Montgomery *et al*. 2001).

1.2.3 Limitation concepts and definitions

Forces acting at multiple spatial scales limit a species' distribution and abundance (Dickinson *et al*. 2007). Some of the most fundamental questions in ecology relate to understanding those limiting factors, and how a species might respond to compensate for negative or positive feedback as a result of them. Recruitment limitation in plant literature has traditionally followed a dichotomous paradigm, where broadly speaking, a plant is either "seed" or "establishment" limited (Poulsen *et al*. 2007). This viewpoint is too simplistic (Clark *et al*. 2007), and a movement that defines seedling recruitment more holistically with a continuum along which the strength of limitation moves with seed input is more ideal.

Seed limitation has recently been recognised as a more important factor in plant species recovery than previously considered (Blomqvist *et al*. 2003, Ozinga *et al*. 2009). Seed limitation can be divided into four definitions: fecundity limitation, where seedling abundance can be increased when seeds are added (Turnbull *et al*. 2000); dispersal limitation, where suitable microsites for establishment and germination are not occupied by seeds; herbivore limitation, whereby herbivore exclosure cages can result in the increased recruitment of seedlings; and microsite limitation, which occurs if added seeds do not result in increased recruitment of seedlings (Rey *et al*. 2006). Munzbergova and Herben (2005) also discuss habitat limitation, which is essentially the spatial extension of microsite limitation. Habitat limitation is when a species' distribution in a landscape is hindered by a lack of suitable and available habitats (Munzbergova and Herben 2005). In this thesis, I refer to seed limitation hereafter as "a population that has fewer individuals than possible because seeds fail to arrive at saturating densities at all potential recruitment sites" (Clark *et al*. 2007, p128). Figure 1.1 outlines a hypothetical situation of the number of seeds at a given site relative to carrying capacity and dispersal distance away from a parent tree. Seed density drops off with dispersal distance away from the parent, as seeds are failing to arrive at those potential recruitment sites.

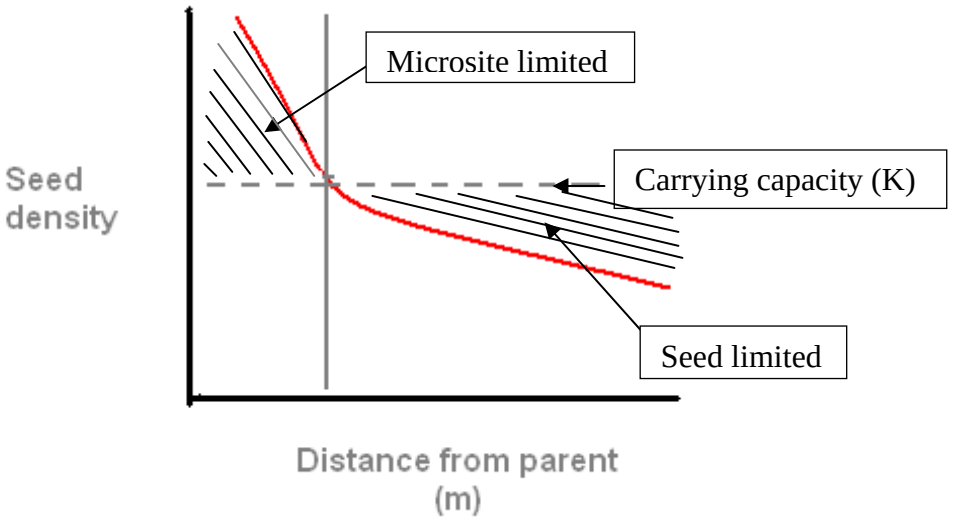


Figure 1.1: Diagrammatical representation of microsite and seed limitation in a plant species. The middle curved line is the number of seeds at a site. Diagram adapted from Poulsen *et al*. (2007).

Seed limitation is becoming frequently more evident in pollen limited populations (Robertson *et al*. 1999). In 1990, Crawley stated plant populations are more limited by microsite limitations than seed limitation. Yet in 1992, Eriksson and Ehrlen found evidence for seed limitation in 9 out of 14 species, and later, Ackerman *et al*. (1996) improved seedling recruitment in an epiphytic orchid by supplementing pollination. Turnbull et al. (2000) reviewed seed limitation studies where both seedlings and adults were recorded, and found that 64% of sites contained seedlings, while only 23% contained adults. This indicates that conditions for establishment are often more stringent than conditions for germination. In addition, recent studies have suggested that some species have seeds and seedlings absent from apparently suitable sites (Turnbull *et al*. 2000). A combination of seed and microsite limitation indicates that increasing both number of seeds and availability of microsites will lead to increased recruitment (Eriksson and Ehrlen 1992).

Few pollination limitation studies go on to consider the effect of seed limitation (Ashman *et al*. 2004), which is outlined by Bond (1994) as a condition to determining whether mutualisms matter. Kelly *et al*. (2007) is one of the few recent studies that consider pollen and seed limitation in the same species, in this case *Peraxilla tetrapetala*, an endemic New Zealand mistletoe. They conclude that the reduction of native pollinating

birds by introduced carnivorous predators has led to the pollen and seed limitation in *Peraxilla tetrapetala*, and trapping of predators should result influence the number of adult mistletoes.

1.3 *Fuchsia excorticata*

1.3.1 Overview of the study species

Fuchsia excorticata (tree fuchsia/ kotukutuku) is a common and widespread New Zealand native tree. *F. excorticata* can grow up to 14 m tall, and have a trunk diameter up to 1 m in very old trees, (but is usually 60 – 80 cm diameter at breast height (DBH)), making it the world's largest fuchsia (Salmon 1980). It is common throughout the country from sea level to 1060 m, but mostly found in moist lowland and mid-mountain regenerating forests, where it can be locally dominant (Dawson and Lucas 2000). It is also commonly seen growing on stream banks and is one of New Zealand's few deciduous native trees. It has attractive flowers, fruit (konini) and foliage that draw nectar and fleshy-fruit eating songbirds such as tui, bellbird and silvereye.

Fuchsia is in the Onagraceae, which has between 100 – 110 species worldwide. Most occur in central and southern America. There is one species in Tahiti, and three species in New Zealand (Godley and Berry 1995). *F. procumbens* is a prostrate shrub and *F. perscandens* is a sprawling shrubby liana. *F. excorticata* is the only species globally that grows in a woody tree form. It is a major colonising species in New Zealand, and plays an important role in stabilising land slips and facilitating secondary succession of well lit, disturbed sites (Wardle 1964, Burrows 1995).

1.3.2 Possum browse and the declining distribution of *Fuchsia excorticata*

F. excorticata is a preferred species of possums (*Trichosurus vulpecula*) (Rose *et al*. 1993, Owen and Norton 1995, Pekelharing *et al.* 1998, Sweetapple *et al*. 2004) due to the high palatability as well as its high nutritional values (P, N, K, Mg and Ca) of its foliage and fruit (Sweetapple and Nugent 1999).

Past studies have documented the widespread death of canopy *F. excorticata* in seral forests due to possum browse (Rose *et al*.1993, Pekelharing *et al*. 1998, Sweetapple and Nugent 1999, Sweetapple 2003, Sweetapple *et al*. 2004), which overall has lead to a declining density of adult *F. excorticata* trees throughout much of its range. Browse damage can range from partial defoliation, dieback, and death of individual trees to localised elimination of whole fuchsia stands (Batcheler 1983, Campbell 1984). Pekalharing *et al*. (1998) show a clear pattern of decreasing foliage cover indices in *F. excorticata* with increasing trap catch of possums (mean number of trapped possums over a predetermined number of trap nights (Brown and Thomas 2000). A foliage cover index (FCI) is the percentage of foliage cover in the crown of each trunk (Pekalharing *et al*. 1998). So when possums are present in mixed-broadleaf forest where *F. excorticata* is present, dieback of adult *F. excorticata* is likely to result in local decline of the species' density. Thus, establishment of new seedlings is especially important to replace dying adults (Robertson *et al*. 2008).

Large *F. excorticata* trees can re-establish their canopy condition over time if possum densities are reduced to <5% of the residual trap-catch index (RTI) (Rose *et al*. 1993, Pekalharing *et al*. 1998). Correspondingly, if possum densities increase above 25% RTI, *F. excorticata* defoliation is increased (Pekalharing *et al*. 1998). However, Urlich and Brady (2005) observed significant possum browse damage at a 15% RTI, suggesting the threshold of possum numbers to cause substantial damage is lower than predicted by Pekalharing *et al.* (1998). There appears to be some inconsistency in browse levels of *F. excorticata* at varying sites. Sweetapple and Nugent (1999) studied *F. excorticata* palatability across different provenances to determine what caused the bias in palatability of browsed *F. excorticata* in forests where possums had been present for a considerable amount of time. Captive possums did not display any preference for foliage from any particular area, nor was there any genotypic variation between specimens collected from different sites. It is therefore suggested that phenotypic variation and situational differences, such as alternative and more attractive food sources, can lead to browse reductions at particular sites, not the palatability of *F. excorticata*.

F. excorticata can provide a useful tool in indicating possum numbers and forest function. The Department of Conservation monitored *F. excorticata* stands in the Tararua range between 1994 and 2004 to determine the effectiveness of possum control, and

found that it suffered significantly more defoliation, more basal stem area loss, and greater mortality in untreated (no possum control) areas than treated (possum control) areas (Urlich and Brady 2005). Even though natural self-thinning and old-age mortality due to limited space and resource competition may have exacerbated the rate of stem loss in their study (Coomes *et al*. 2003), it is considered that *F. excorticata* suffered under high possum densities in untreated areas.

Beech (*Nothofagus* spp.) are a non-preferred genus for possums (Wardle 1984), however as *F. excorticata* and beech frequently co-occur, the browse index of *F. excorticata* can still help determine the abundance of possums in a beech dominated or co-dominated forest (Rose *et al*. 1993). For example, associated seral *F. excorticata* in Rose *et al*. (1993) suffered substantial dieback in the mid Arawata and lower Waiatoto Valleys in South Westland, where canopy dieback of *Nothofagus* was not evident. When *F. excorticata* co-occurs with more highly preferred canopy species such as southern rata (*Metrosideros umbellata*), overall depletion of the forest in all canopy tiers by possum browse is more apparent (Rose *et al*. 1993). Either way, *F. excorticata* provides a useful tool to help determine possum densities in any forest type it occurs in.

1.3.3 Breeding system – gender dimorphism

Gender dimorphism is exhibited to some extent in 83 seed plant genera (23%) in New Zealand (Webb *et al*. 1999). The condition, in which male, female or hermaphrodite reproductive organs occur on separate plants, is strongly correlated with fleshy fruits and woody habits, both of which are displayed by *F. excorticata*.

F. excorticata is gynodioecious, which means it has separate hermaphrodite and female plants. Gynodioecism occurs in 7.2% of the genera in New Zealand (Webb *et al*. 1999). Current research is being conducted to determine whether *F. excorticata* is suffering from inbreeding depression when hermaphrodite flowers self pollinate (J. Ladley/D. Kelly *pers. comm.*). Other New Zealand gynodioecious species, such as *Hebe subalpina* have been proven to be experiencing inbreeding by selfing hermaphrodites, which ultimately affects the evolution and maintenance of gynodioecy as a breeding system (Delph and Lloyd 1996). Wilson and Harder (2003) have shown the benefits of dioecy over

hermaphroditism (in gynodioecy) because of reproductive uncertainty surrounding pollination limitation.

Herkogamy (separation of anthers and stigma in space) varies on hermaphroditic *F. excorticata* plants, consequently leading individual plants to be more or less susceptible to selfing (Robertson *et al*. 2008). Through herkogamy, a flower can reduce the potential for inbreeding. Alternatively, dichogamy (separation of pollen production and stigma receptivity in time) can help reduce selfing. The frequent occurrence of dichogamy and herkogamy in self-compatible species emphasises that selection for enhanced pollination efficiency is beneficial (Webb and Kelly 1993).

1.3.4 Floral colour change

Further complexities arise in *F. excorticata.* An age-dependent colour change occurs from green flowers to red flowers. The green flowers contain pollen and nectar, and once flowers have been pollinated they take 3 – 5 days to turn red (Delph and Lively 1989). It is hypothesised that an instantaneous colour change does not occur because it takes approximately 3 days for the pollen tube to reach the ovary from the stigma, so the flowers change colour rather than drop off to be sure of successful pollination. This mechanism increases foraging efficiency, as pollinators have learnt that no reward is associated with red flowers (Delph and Lively 1985).

1.3.5 The potential for seed limitation in *Fuchsia excorticata*

A lack of sufficient pollination can lead to seed limitation because of restricted fruit set. It is important to determine if *F. excorticata* regeneration is seed limited, principally because it suffers from pollination limitation and a declining adult distribution from possum browse (Robertson *et al*. 2008). However, pollination limitation will not be of any significance if *F. excorticata* is not seed limited, due to the seeds in the seed bank producing sufficient numbers of seedlings for regeneration of the species.

The decline in pollination mutualist service is probably due to the decline of honeyeater bird species that visit the fruit and flowers (Robertson *et al*. 2008). Bellbird, tui and silvereye are the three main bird visitors to *F. excorticata* flowers (Delph and Lively

1985, Kelly *et al*. 2006). Stitchbird also are notably attracted to *F. excorticata* (Robertson *et al*. 2008), but are now extinct from the mainland so cannot be regarded here as a reliable pollinating species. Stitchbird are therefore "functionally extinct" as described in Sekercioglu *et al*. (2004) (Chapter 1.1). Kereru also visit the fruit (McEwen 1978). Bellbird and tui abundance has declined on the New Zealand mainland over the past 150 years (Robertson *et al*. 1999), which means less abundance of primary mutualist partners, and an impact on essential ecosystem services.

The Pollination limitation index (PLI) is a scoring mechanism devised by Larson and Barrett (2000) that indicates the severity of pollination limitation. In *F. excorticata* the mean PLI was 0.17 (out of 1) for hermaphrodites and 0.40 for females (Robertson *et al*. 2008). *Fuchsia excorticata* hermaphrodites showed smaller degrees of pollen limitation, and are self-compatible, as opposed to *F. excorticata* females which were more strongly pollen limited.

Robbing of nectar occurs in *F. excorticata* which can result in inefficient pollination and can subsequently deter other pollinators from visiting the flowers (Delph and Lively 1985). The hypanthium tube in *F. excorticata* hermaphrodites is about 20mm long, and is thought to be too long for a silvereye beak (14.3mm average) to reach the nectar from the flower (Delph and Lively 1985). Female flowers are about half as long, so nectar can easily be reached by silvereyes (Delph and Lively 1985). Silvereyes have frequently been observed piercing holes in the side of hermaphrodite flowers in order to reach the nectar, failing to achieve successful pollination. Bumblebees then use the holes made by the silvereyes, rob the nectar and again do not provide an effective pollination service (Delph and Lively 1985).

Seeing visitors to a flower is not a certain proof of pollination (Godley 1979, Clout and Hay 1989). So it is important to gain information on seed set, as reduced fruit set from lack of sufficient pollination or dispersal mutualisms will only affect a species' population if it is seed limited (Bond 1994). When a species is pollen limited and fewer seeds are produced, they undergo reduced competition to colonise the "safe sites"/suitable microsites (Kelly *et al*. 2010). Additionally, if density dependent seedling deaths are commonplace, then the reduced fruit set from pollination limitation may not affect recruitment (Robertson *et al*. 1999, Kelly et al. 2007).

Turnbull *et al*. (2000) found that seed limitation tends to occur more commonly in early successional habitats and early successional species. *F. excorticata* is a partially seral species which is later replaced by other trees (Robertson *et al*. 2008), highlighting the need for production and dispersal of viable seeds. *F. excorticata* is known to have a seed bank (MacDonald 1985, Burrows 1995, Bartholomew *pers. comm.*). If seeds are already widespread in the seed bank, it is less likely that it will be seed limited.

Mean seed size varies over a wide range among species (Moles *et al*. 2000). Small seeded species are able to produce a high quantity of seed mass through production of many small seeds with low probability of successful establishment, whereas large seeded species produce fewer seeds, with a higher chance of successful establishment (Moles *et al*. 2000). Bigger seeds are thought to be able to cope with limited light and water better, as they can rely on stored resources for longer without succumbing to drought, shade, or herbivory (Westoby *et al*. 1996).

F. excorticata has small seeds. In a sample of 100 fruit, the mean seed mass was 0.07 mg, length 0.62 mm ± 0.06, and width 0.28 mm ±0.06 (Burrows 1995). Burrows (1995) found 266 ± 92 seeds per fruit, with a fruit size of 11.6 mm ± 2.5. The smallness of the seeds means seedlings are small and fragile upon germination, so may struggle with establishment (Parciak 2002). Furthermore, the small seeds have little food storage capacity, reducing the potential for the seed to remain dormant for a long period of time (Burrows 1995).

1.3.6 Restoration

Traditional conservation measures such as habitat protection are progressively becoming inadequate in halting diversity losses (Ozinga *et al*. 2009). Improving habitat quality is valuable, yet it does not always specifically address the species at risk, and the further problems the species are facing with a declining distribution. “What escapes the eye, however, is a much more insidious kind of extinction: the extinction of ecological interactions” (Janzen 1974). By studying seed limitation in *F. excorticata*, restoration of the forest communities of which *F. excorticata* is an integral part of in New Zealand can focus on the ecological interactions that Janzen describes above.

If *F. excorticata* is found to be seed limited, the species is likely to benefit from longer term studies of pest control of the predators of the mutualist partners in the pollination and dispersal systems, which would help managers devise a more integrated community based approach to *F. excorticata* conservation.

1.4 Overall objectives of this thesis

Safe sites for regeneration are uncertain in time and space (Kelly *et al*. 2004). It is predicted that many species will be found to be both seed and microsite limited if studied thoroughly (Eriksson and Ehrlen 1992). Little is known about whether *F. excorticata* regeneration is limited by seed supply (seed limitation) or some other environmental or ecological factor such as the availability of microsites (establishment limitation) (Clark *et al*. 2007), or, a mixture of the two. Empirical studies of seed rain and seed banks in conjunction with seed limitation are important to help determine the relative importance of the limitations, and the variation within them (Poulsen *et al*. 2007).

Kelly *et al*. (2007) call for more synonymous studies between pollen and seed limitation, as management regimes decided by one form of limitation may not be necessary, because a species may be able to compensate for one limiting life history trait through another positive one. By studying the seed regeneration capabilities in *F. excorticata,* I hope to verify whether its pollination limitation and declining distribution through possum browse is of major concern to the long term stability of the species, and what ecological and conservation implications may occur as a result of these limitations. Seed limitation seems unlikely in *F. excorticata* because of its small seeds and persistent seedbank, however empirical information is necessary.

Hypothesis 1: Do sites with continuous pest control have higher numbers of native birds that provide a better pollination and dispersal mutualism service to *F. excorticata*?

Hypothesis 2: Do *F. excorticata* seedlings naturally favour particular microsites with particular environmental conditions?

Hypothesis 3: Does the distribution of *F. excorticata* seeds in the seed bank decline with dispersal distance away from a parent tree? Is there an effect of density of adult fuchsia at the site or numbers of birds at each site?

Hypothesis 4: Is *F. excorticata* seed limited? Does addition of *F. excorticata* seed produce more seedlings than plots without seed addition? Do sites with more intensive pest control have better regeneration conditions for *F. excorticata* than sites with low intensity of pest control? Is there an effect of excluding herbivores from seedling plots? Does germination of seeds decrease over dispersal distance?

Chapter 2: Study sites and Bird densities

2.1 INTRODUCTION

2.1.1 Site selection

Study sites were chosen to reflect a range of South Island conditions under varying management schemes. Sites needed to be large enough to keep edge effects small. Potential field sites around the South Island were scouted out in November and early December 2008. Four final sites were confirmed within two regions in order to be able to generalise. Within each region there was a site with a high intensity of pest control, and a low intensity of pest control. In the Nelson region St Arnaud/Lake Rotoiti and Grampians Reserve, Nelson City (high and low pest control respectively) and two in Canterbury, Hinewai Reserve and Mt Thomas (high and low pest control respectively). Each region had one site with 'high' and one with 'low' densities of mature fuchsia trees. I defined 'high density' of *F. excorticata* as where *F. excorticata* was one of the predominant tree species over patches of approx 50 m^2. Conversely, 'low density' is when *F. excorticata* is present, but not a predominant species. The Canterbury sites lie approximately 100km apart, and Grampians Reserve lies approximately 70km north of St Arnaud in the Nelson region (Figure 2.1).

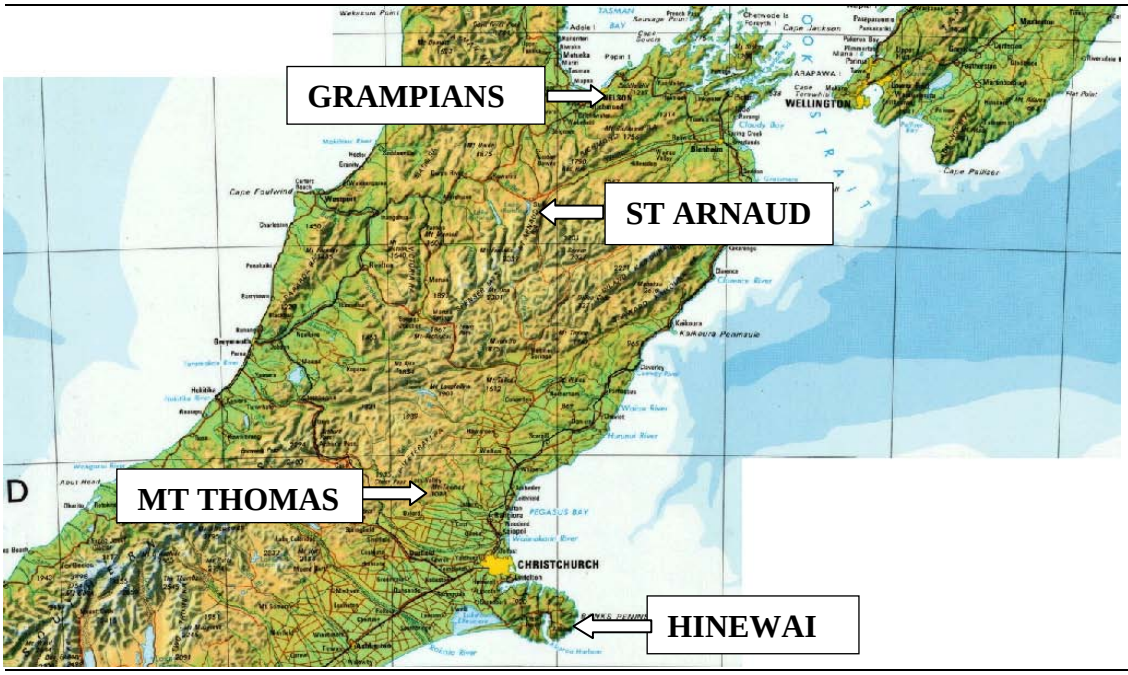


Figure 2.1: Overview of the Northern South Island showing location of my four study sites.

Table 2.1: Site information and relative *F. excorticata* and bird densities

Site	**Region**	***Fuchsia* density**	**Pest control intensity**	**Altitude**	**Lattitude/ Longitude**
Hinewai	Canterbury	High	High	400 m	43° 48'13" S 173° 1'14" E
Mt Thomas	Canterbury	Low	Low	300 m	43° 11'60" S 17 20’04" E
St Arnaud	Nelson	Low	High	620 m	41° 48'25" S 17 50'72" E
Grampians	Nelson	High	Low	240 m	41°17'28" S 173°16'40" E

2.1.2 Hinewai Reserve, Banks Peninsula

Hinewai Reserve on Banks Peninsula (Akaroa Ecological District) is owned by the Maurice White Native Forest Trust. The initial reserve patch was bought in September 1987, with only 109 hectares of weedy overgrown farmland with pockets of regenerative bush, but has expanded to 1230 hectares (as at February 2009) (Wilson 2009. *pers. comm*.). The area is privately managed with strong underlying conservation values for the protection and regeneration of native flora and fauna. The reserve lies in the steep Otanerito Valley and therefore covers a large altitudinal range, from 20 m above sea level (a.s.l) at the Otanerito Homestead to 803 m (a.s.l) at Stony Bay Peak (Figure 2.2). The visitors centre is around 400 m a.s.l. Soils are moderate to highly fertile (Wilson 1994). Rainfall ranges from 1800 mm/year at the higher altitudes to 1400 mm/year at the bottom of the valley.

Vegetation on the reserve varies from native red beech (*Nothofagus fusca*) forest, to kanuka *(Kunzea ericoides*) forest, and second growth mixed broadleaf forest (*F. excorticata,* mahoe – *Melicytus ramiflorus,* five-finger – *Psedopanax arboreus,* pate – *Schefflera digitata.*) (Wilson 2009, Hinewai visitors information.). About 60% of the reserve is classified as ‘scrub’, with extensive patches of gorse (*Ulex europaeus*), broom (*Cytisus scoparius*) and young kanuka. The Hinewai manager, Hugh Wilson projects that by 2050 Hinewai should have regenerated to around 95% second growth forest, 4% old growth forest and 1% tussock, shrubland and scrub that persists on rocky bluffs, provided fire events can be excluded (Wilson 1994).

Figure 2.2: Map of Hinewai Reserve near Akaroa. Highlighted section is the boundary of the reserve, and the pink circle is where my study trees were located. The Hinewai visitor centre is at approximately 450 m a.s.l. Sourced from NZMS 260 series, blue grid is equivalent to 1 km.

Possums (*Trichosurus vulpecula*), goats (*Capra hircus*), hares (*Lepus europaeus occidentalis*), rabbits (*Oryctolagus cuniculus cuniculus*), hedgehogs (*Erinaceus europaeus occidentalis*), rats (*Rattus rattus, Rattus norvegicus*), mice (*Mus musculus*), stoats (*Mustela erminea*), ferrets (*Mustela furo*), cats (*Felis catus*) and weasels (*Mustela nivalis vulgaris*) (King 2005) are all present at Hinewai (Wilson 2009), and pose a detrimental effect to the natural regeneration of the healthy forest ecosystem. Bellbirds, brown creepers (*Mohoua navaeseelandiae*), tomtits (*Petroica macrocephala*), kereru, grey warblers (*Gerygone igata*), fantails (*Rhipidura fuliginosa*) silvereyes, blackbirds (*Turdus merula*), thrush (*Turdus philomelos*), finches (*Fringilla coelebs, Carduelis chloris, Carduelis carduelis*), redpoll (*Carduelis flammea*) and magpies (*Gymnorhina tibicen*) (Heather and Robertson 1996) are all common bird species. Tui have been virtually absent from Banks Peninsula for about 20 years, so 30 birds were released at Hinewai in April 2009 in an effort to reintroduce them to the area (Banks Peninsula Conservation Trust 2010). Intensive pest control and some poisoning occurs that mainly targets goats and possums, so Hinewai is considered to be an “intensive pest control” area in my study. For the tui project, 100ha of land was controlled for all possible pests, including mustelids and rats. Although rats are not targeted as pests, they have been

observed to eat brodifacoum bait that was intended for possums (H. Wilson pers. comm. 2010).

2.1.3 Mt Thomas, Canterbury

The Mt Thomas Forest Park covers 10,800 hectares between the Ashley and Okuku Rivers in the Canterbury foothills. It is bordered by the Lees Valley to the north-west, and the Canterbury Plains to the south and east. It is Crown conservation land managed by the Department of Conservation (DOC) in the Waimakariri Ecological District. In January 2009 a cyanide poison drop was performed by the Animal Health Board to target possums carrying bovine tuberculosis. DOC does not perform any pest control and has not done so for a number of years (C. Hogan, DOC Waimakariri, *pers. comm*. 2009). Therefore, Mt Thomas is considered a "low intensity pest control" site. Both a deer and a stoat were seen during daylight at the site.

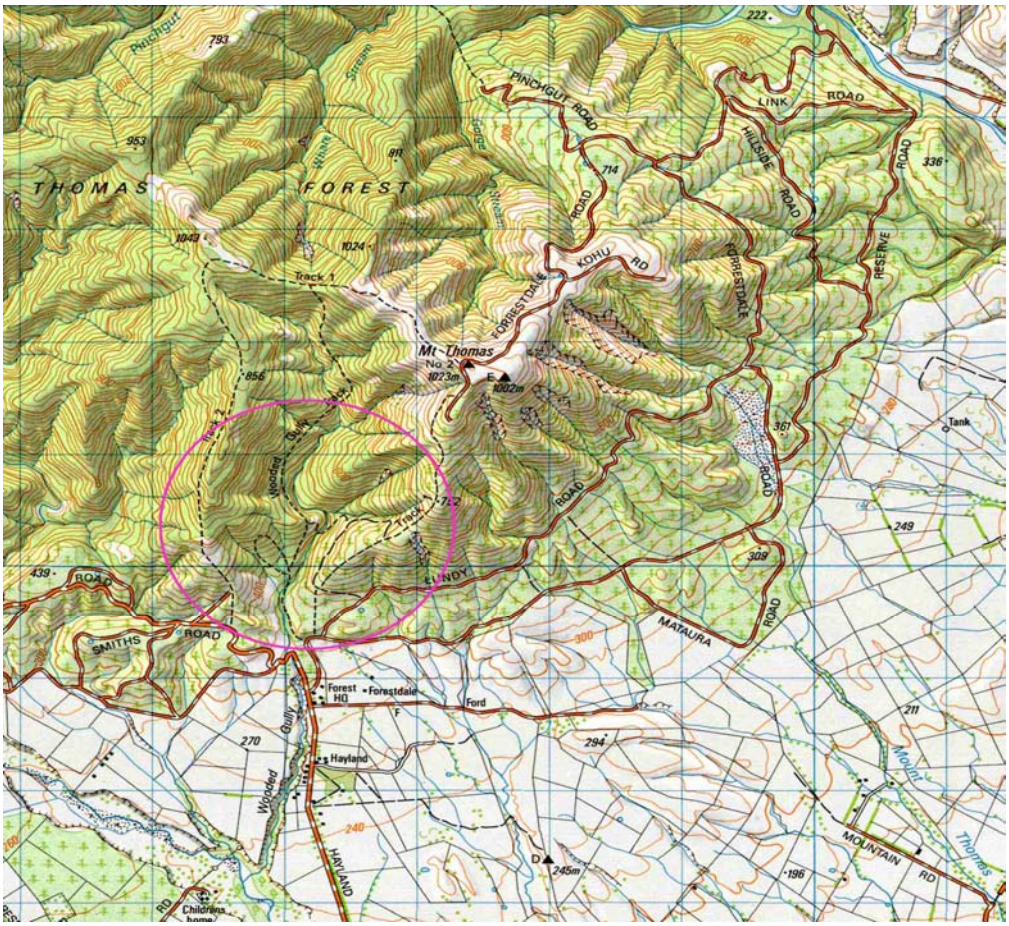


Figure 2.3: Map of Mt Thomas Forest showing the general location of my study site inside the pink circle. Sourced from NZMS 260 series, blue gridlines are equivalent to 1 km.

This site is located near the Wooded Gully car park area (Figure 2.3). Most soils in the Canterbury High Country have a deep loess base and free draining gravel bases, but have good water storage capacities. These dry eastern foothills average between 900 – 1400 mm rainfall per annum. Summer drought is common and the main limiting factor in Canterbury agriculture and forestry.

Vegetation is predominantly black beech (*Nothofagus solandri* var. *solandri*), with several species of broadleaf hardwood such as mahoe, five-finger, *Coprosma robusta* and tree fuchsia, as well as scrub areas with broom and gorse (Wiser *et al.* 1997). Other weeds such as blackberry (*Rubus fruticosus*) and Himalayan honeysuckle (*Leycesteria formosa*) are common throughout. There is also an abundance of naturalised cherry trees (*Prunus* spp.).

2.1.4 St Arnaud, Nelson Lakes

St Arnaud/Lake Rotoiti is in Nelson Lakes National Park, and was my only site in a National Park. The Rotoiti Nature Recovery Project (RNRP) is a large scale ‘mainland island’ attempt at restoring approximately 5000 hectares of native forest to a fully functioning beech honeydew forest ecosystem (Paton *et al.* 2007). Intensive trapping and pest control targets stoats, possums, deer, rodents and wasps at Rotoiti.

The area has an alpine climate, with around 2000 mm of rain per annum. During the last ice age (around 12,000 years ago) glacial movement carved broad, steep-sided valleys, lakes, ridgelines, and alpine basins and tarns.

The RNRP includes 825 hectares of mixed beech forest on the eastern side of Kerr Bay, including red (*Nothofagus fusca*), silver (*Nothofagus menziesii*) and mountain beech (*Nothofagus solandri* var. *cliffortioides*). Broadleaf (*Grisilinea littoralis*), marbleleaf (*Carpodetus serratus*) and small leafed coprosma are common in the understory. *F. excorticata* is at low densities under the beech canopy, and mainly found on the flat areas at the start of the Bellbird walk or in open streambeds on the Honeydew and Lakehead tracks (Bartholomew 2008, R. Bell *pers. obs.*, Figure 2.4).

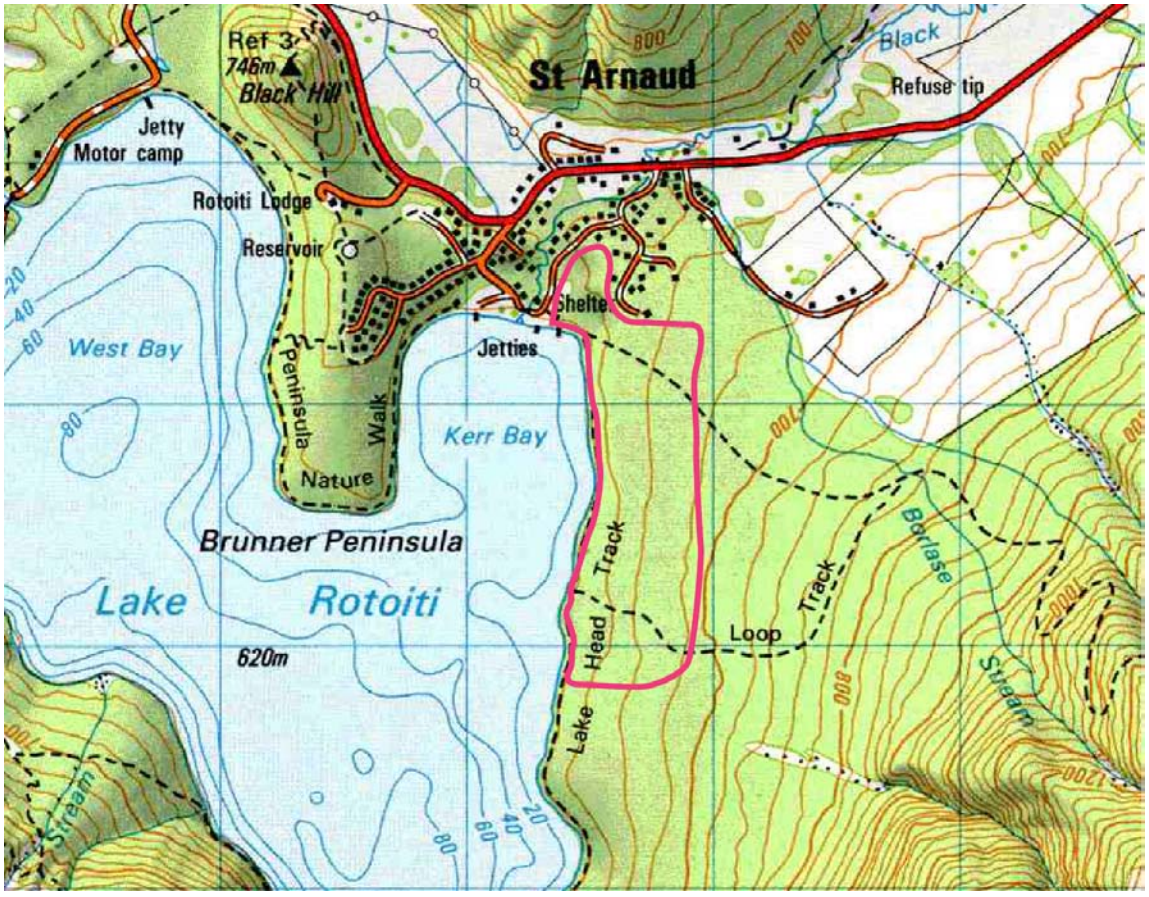


Figure 2.4: Map of St Arnaud showing the general location of my study site. My study trees are within the pink border. Sourced from NZMS 260 series, blue gridlines are equivalent to 1 km across.

2.1.5 Grampians Reserve, Nelson

The Grampians reserve in Nelson city is an area of mixed exotic and native secondary succession forest in the hills behind Nelson city. It is managed and owned by the Nelson City Council. My site was accessed via the Bishopdale side (Figure 2.5). Nelson city receives an average of 986mm of rain per year, and over 2500 sunshine hours, so has a generally warm and dry climate.

There were two plantations of blackwood (*Acacia melanoxylon*) growing near my site, and other areas of pine, eucalyptus, oak (*Quercus robur*), feijoa (*Feijoa sellowiana*), ash (*Fraxinus spp.*), cedar, maple (*Acer spp.*) and sequoia. The Grampians' proximity to the city means that garden escapees such as holly (*Ilex aquifolium*) have become naturalised in the reserve. Other weeds such as banana passionfruit (*Passiflora mixta*), old man's beard (*Clematis vitalba*), black nightshade (*Solanum nigrum*) and Himalayan

honeysuckle are widespread (Nelson City Council website). Common native species include kawakawa (*Macropiper excelsum), F. excorticata,* titoki (*Alectryon excelsus*) and wineberry (*Aristotelia serrata*) (R. Bell *pers. obs*).

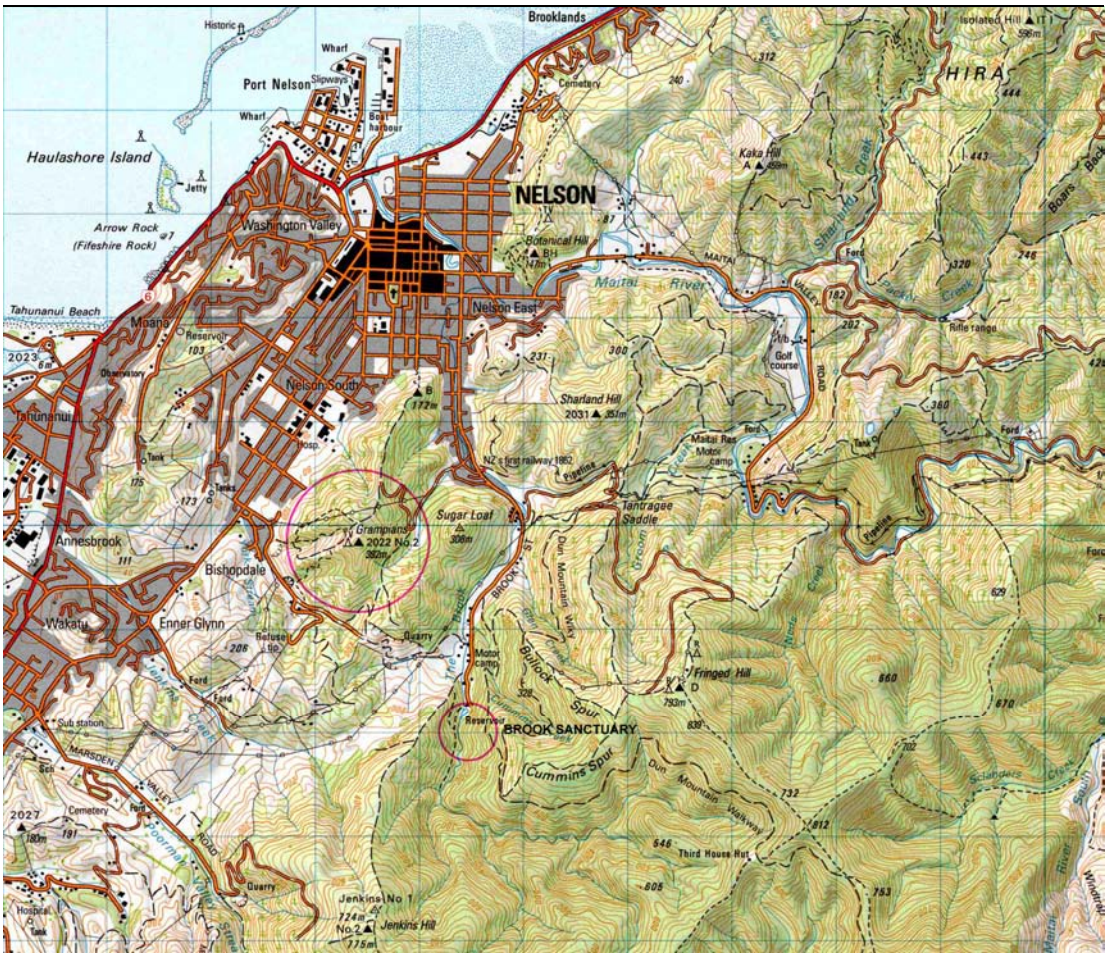


Figure 2.5: Map of Nelson city showing the general location of my study site, the Grampians reserve in the large pink circle. The small pink circle shows the Brook Sanctuary, which is where *F. excorticata* fruit was sourced from (see Chapter 5). Map sourced from NZMS 260 series, blue grid is equivalent to 1 km.

2.1.6 Pollen limitation

Females at (or near) my field sites for this study are carrying less than 1% pollen, whereas hermaphrodites are carrying up to 20% (Table 2.2) in 2008. The self-compatibility in *F. excorticata* hermaphrodites is beginning to show signs of inbreeding

depression (Robertson *et al.* 2008), which are worth less to regeneration than crossed individuals.

Table 2.2: Average pollen load of *Fuchsia excorticata* hermaphrodites and females at sites close to or at my sites. (Scale: 0 = 0%, 1 = 1-5%, 2 = 6-20%, 3 = 21-40%, 4 = 41-100%) Source: National Pollination Survey 2008.

Location	Region	Pollen Herm.	Pollen Female	Pollen average
Maitai	Nelson	1.21	0.53	1
Kerr Bay	Rotoiti NRP	0.97	0.24	0.73
Mt Richardson	Canterbury	2.39	0.82	1.87
Hinewai	Banks Peninsula	2.63	0.54	1.93

2.2 METHODS

2.2.1 Bird densities

Study sites were chosen to reflect varied levels of pest control, ranging from very intensive mainland island control (the RNRP at St Arnaud), to occasional removal of thriving weeds by the city council and local volunteers (Grampians). It is assumed that higher intensity of pest control leads to a greater abundance of birdlife so a series of bird counts were undertaken to confirm this hypothesis.

Bird visitation rates to *F. excorticata* flowering adults were recorded in spring 2009 following the methods of Robertson *et al.* (2008). At each site, 6 observation stations were selected, where any avian visitor to the chosen *F. excorticata* adult(s) would be clearly visible to me. In total, between 48 – 57 minutes were spent at each station. Observation sessions were timed to last for 10 minutes, however Hinewai had four extra minutes recorded, and Grampians eleven (Table 2.3). Each 10 minute block was performed at a different time of day, to ensure that recording covered any possible peaks and lulls in bird activity throughout the day. At Hinewai, thrush, brown creepers and tomtits were observed on the *F. excorticata* trees, however as these species are not part of the main honey eating guild of pollinators of *F. excorticata* flowers, they were excluded from the analysis. Tui, bellbird and silvereye were the main flower visitors.

The number of flowers on the visible part of the observation tree was estimated to allow calculation of the visitation rate per flower, and thereby a comparison of bird visitation at each site.

To measure general diversity and abundance of birds, conventional 5 minute bird counts (5MBC) (Dawson and Bull 1975) were performed at each observation station. Number and species of birds that were heard or seen within 100 m in the first 5 minutes of the visitation observations were recorded. At least five repeat counts were completed at each station, totalling 30 repeats at Mt Thomas, St Arnaud and Grampians. Hinewai counts totalled 32 repeats. The 5MBC allow for simple comparison to past and future studies as they are widely used.

2.3 RESULTS

2.3.1 Bird visitation

Following bird visitation observations the Grampians was the site with the highest visitation rates per flower (Table 2.3) which is surprising considering the low intensity of pest control. Hinewai and St Arnaud are near equal, and Mt Thomas has much fewer and shorter visits per flower (Table 2.3) indicating a declined mutualist service for *F. excorticata*.

Hinewai, St Arnaud and the Grampians had higher total visitation to flowers than Mt Thomas (Table 2.3), although non-significant ($P = 0.11$) due to the variance around the mean. In the Nelson sites where tui were present, they represented over half of the visits to *F. excorticata* flowers (Table 2.4). Silvereye only really performed a noteworthy portion of the visits at Hinewai. Tui are absent from Mt Thomas, and no silvereye were observed visiting *F. excorticata*, so all visits there were from bellbirds. Although Hinewai has recently had tui released, none were observed visiting *F. excorticata.* Silvereyes were observed at 4 out of 6 observation stations at Hinewai, although bellbirds were most common (Table 2.4), in contrast to the findings of Robertson *et al.* (2008) at this same site. Pest control intensity had no significant effect on bird visitation to *F. excorticata* flowers ($P = 0.888$), neither did *F. excorticata* density ($P = 0.1143$).

Table 2.3: Bird (Tui, bellbird and silvereye combined) flower visitation rate to *F. excorticata* trees at each study site. There were six observation stations at each site.

Site	Flower visitation rate sec/flower/ hour	Standard error mean (SEM)	Total observation time (mins)
Hinewai	0.49	0.06	304
Mt Thomas	0.09	0.03	300
St Arnaud	0.54	0.21	300
Grampians	1.02	0.5	311

Table 2.4: Percentage of visits at each site by the three main pollinating mutualists: Tui, Bellbird and Silvereye.

Site	Tui	Bellbird	Silvereye	Total duration of all visits (secs)
Hinewai	0	73	27	3054
Mt Thomas	0	100	0	427
St Arnaud	55	45	0	1216
Grampians	55	39	6	2658

2.3.2 Five minute bird counts

Only four species make up the majority (84%) of bird counts in the 5MBCs, (tui, blackbird, bellbird and grey warbler), although there is presence of 16 other species (Table 2.5). Bellbirds were the most common species across all sites, with an average of at least three individuals heard or seen per 5MBC. They were most common at St Arnaud, with nearly six individuals seen and/or heard each count. The Grampians was the only site where bellbirds were not the most common, with blackbirds and tui more common than bellbirds.

Observations from the 5MBC showed differing results to the visitation rates. High pest control sites had over twice as many observations of honeyeating birds than the sites with low pest control (Figure 2.6, $P < 0.001$).

Table 2.5: Average number of all bird species observed in 5 minute bird counts at all sites (averages to two decimal places).

Species	Grampians	Hinewai	Mt Thomas	St Arnaud	Total
Bellbird	0.80	3.50	2.83	5.83	3.24
Blackbird	1.50	0.57	1.20	0.97	1.06
Brown Creeper	0.00	0.67	0.00	0.00	0.17
Fantail	0.07	0.13	0.03	0.00	0.06
Finch	0.03	0.23	0.00	0.03	0.08
Grey Warbler	0.53	0.93	0.10	0.00	0.39
Harrier hawk	0.00	0.07	0.00	0.00	0.02
Kaka	0.00	0.00	0.00	0.17	0.04
Kereru	0.03	0.10	0.07	0.00	0.05
Magpie	0.00	0.10	0.00	0.00	0.03
Paradise duck	0.00	0.07	0.00	0.00	0.02
Quail	0.00	0.10	0.00	0.00	0.03
Silvereye	0.27	0.23	0.00	0.20	0.18
Skylark	0.07	0.20	0.00	0.00	0.07
Song thrush	0.27	0.00	0.13	0.17	0.14
Sparrow	0.20	0.00	0.00	0.03	0.06
Starling	0.03	0.00	0.00	0.00	0.01
Swallow	0.00	0.17	0.00	0.00	0.04
Tomtit	0.00	0.33	0.00	0.00	0.08
Tui	1.27	0.00	0.00	2.50	0.94

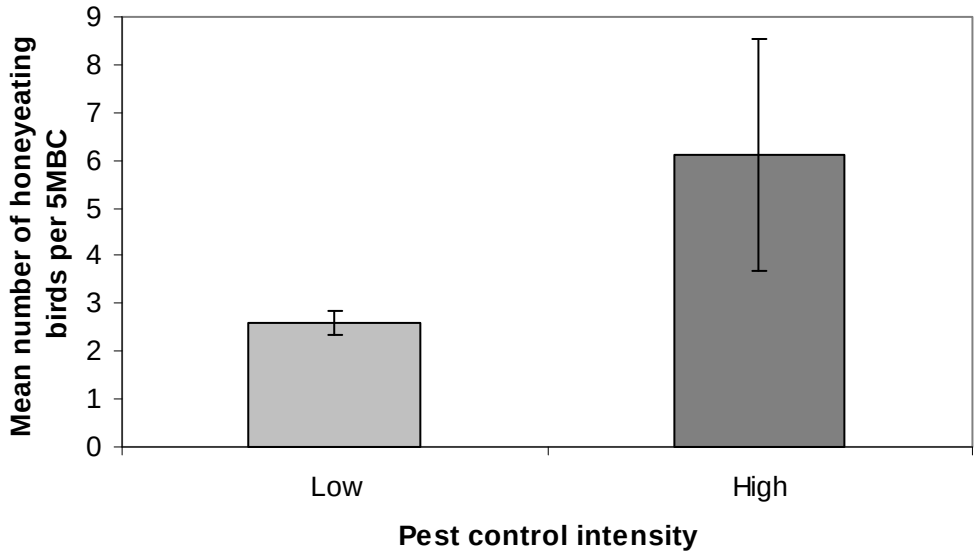


Figure 2.6: Mean number of honeyeating birds (Tui, bellbirds and silvereye) counted in 5 minute bird counts at each site. Total counting time for high pest control sites = 310 minutes, low pest control sites = 300 minutes.

Four separate GLM's were run in R (Version 2.10.1) using poisson error to test the effect of selected variables on the three most common bird species; tui, bellbird and blackbird (Table 2.6a). Pest control significantly affects the number of birds of all three species, although high pest control has a positive effect on bellbird, tui, and all honeyeaters combined thus increasing numbers, but a negative effect on blackbirds (Table 2.6b). Blackbirds are significantly more common in low pest control areas. Region was expected to be, and was, highly significant for tui, as their range does not extend into Canterbury (Table 2.6). Blackbirds were found to be more common in Nelson. Station and replicate count was insignificant for all birds, showing each species is well dispersed around each site, so this variable was removed from the final analysis.

Table 2.6a: Analysis of deviance tables from three separate GLM's using poisson error testing pest control regime, region and their interactions on the three most common bird species, and all honeyeaters (bellbird, tui and silvereye) combined in the 5 minute bird counts.

Bellbird	Df	Deviance	P(>|Chi|)
Pestcontrol	1	79.261	<0.001
region	1	1.128	0.288
pestcontrol:region	1	59.253	<0.001
residuals	116	52.945	
Tui			
pestcontrol	1	15.895	<0.001
region	1	164.969	<0.001
pestcontrol:region	1	<0.001	1
residuals	116	92.595	
Blackbird			
pestcontrol	1	8.674	0.003
region	1	4.188	0.041
pestcontrol:region	1	0.708	0.4
residuals	116	116.94	
All honeyeaters			
pestcontrol	1	95.919	<0.001
residuals	118	143.4	

Table 2.6b: Co-efficient table of above GLM's.

Bellbird
Coefficients:

	Estimate	Std. Error	Z value	Pr(>|z|)
(Intercept)	1.20	0.10	12.04	<0.001 ***
pestcontrollow	-0.16	0.15	-1.10	0.27
regionnelson	0.60	0.12	4.81	<0.001 ***
pestcontrollow:regionnelson	-1.86	0.26	-7.10	<0.001 ***

Tui
Coefficients:

	Estimate	Std. Error	Z value	Pr(>|z|)
(Intercept)	-1.93×10^{3}	1.72×10^{3}	0.01	1
pestcontrollow	3.27×10^{-10}	2.43×10^{3}	1.34×10^{-1}	1
regionnelson	2.03×10	1.72×10^{3}	0.01	1
pestcontrollow:regionnelson	-7.57×-10	2.43×10^{3}	$-3.11 \times 10^{-}$	1

Blackbird
Coefficients:

	Estimate	Std. Error	Z value	Pr(>|z|)
(Intercept)	-0.57	0.24	-2.34	0.02 *
pestcontrollow	0.72	0.30	2.44	0.01 *
regionnelson	0.57	0.30	1.87	0.06.
pestcontrollow:regionnelson	-0.32	0.39	-0.84	0.40

All honeyeaters
Coefficients:

	Estimate	Std. Error	Z value	Pr(>|z|)
(Intercept)	1.50779	0.07751	19.452	<0.001
pestcontrollow	-0.89264	0.09567	-9.330	<0.001

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.'

2.4 DISCUSSION

Of the three New Zealand honeyeater species, tui are known to be more nectarivorous, bellbirds more insectivorous, and stitchbird more frugivorous (Gravatt 1969, Craig *et al.* 1981, Angehr 1986, Murphy and Kelly 2001). However, bellbirds and stitchbirds have a

larger intake of carbohydrates when there is reduced competition from larger territorial birds such as tui (Gravatt 1969, Franklin 1997).

At Craigieburn bellbirds are known to be annual generalists on honeydew, gaining 2 – 45% of their food resource from this carbohydrate rich product of *Ultracoelostoma* spp. (Murphy and Kelly 2001), but they are seasonally dependent on fruit and flowers from nectar rich species when available. As honeydew is not present at Hinewai and the Grampians, bellbirds are likely to rely heavily on the seasonal nectar contribution of species such *as F. excorticata*, especially because it is at high densities.

A possible explanation for the longest mean duration of visits per flowers at the Grampians can be gained from behavioural site observations. More tui were observed visiting *F. excorticata* trees than bellbirds (Table 2.4), and it was noted that tui tended to stay longer in one place than bellbirds, spending more time perching and interacting with other birds. Bellbirds tended to spend the entire length of time they were in a tree moving from flower to flower, and very little social interaction between bellbirds was observed.

Furthermore, the Grampians has a high density of *F. excorticata* trees, of which most are very large and mature and also seemed to have less intense flowering than the trees at other sites. The high *F. excorticata* density (Table 2.1) means that nectar from *F. excorticata* flowers is a much more conspicuous food source from the flowers at the Grampians and Hinewai sites. Birds at St Arnaud are perhaps more accustomed to acquiring food from alternative sources in spring other than *F. excorticata* flowers.

Tui were recorded at St Arnaud as well, but only on the larger trees of *F. excorticata* that were being observed for visitation. As *F. excorticata* is uncommon at St Arnaud, the nectar may not be energetically attractive to forage at. Also, tui seemed and bellbirds spent a lot of time there foraging high in the canopy, above where the *F. excorticata* trees were (R. Bell *pers. obs*).

There were many blackbirds *(Turdus merula*) at all sites (Table 2.5) recorded in the 5MBC, the second most abundant species after bellbirds. Blackbirds are the most widespread avian seed disperser in New Zealand, and along with the silvereye, perform dispersal service for many native and introduced plants (Williams 2006). However, Kelly *et al*. (2006) reported that blackbirds are often overestimated as dispersers of native

plants as they only disperse 3% of all fruits from native plants, while tui, kereru, bellbird and silvereye combined are taking 85%.

Tui and bellbirds were frequently heard and observed at St Arnaud, however their presence was often high in the canopy of the *Nothofagus* forest, and seldom did they spend time in the understory where *F. excorticata* grows, which helps display the inconsistency between the visitation rates and 5MBC. These numbers help to confirm the reliance on food sources other than *F. excorticata* at St Arnaud.

Birds are known to be difficult to quantify in 5MBC because they record conspicuousness, rather than a reliable measure of density (Murphy and Kelly 2001). These counts are therefore a best estimate of what is present at each of my sites, and although difficulties with observations may skew data, they can show general patterns of diversity and abundance, thus serving the purpose of this research.

2.5 CONCLUSION

Although bird visitation rates to *F. excorticata* are not consistent with predictions from intensity of pest control, some explanation can be gained from alternative food sources, prominence of *F. excorticata* in the plant community and competition from other honeyeating birds.

1) There is no relationship between pest control intensity and visitation rate to *F. excorticata* flowers.

2) Honeyeating birds appear to be visiting *F. excorticata* flowers when it is a more conspicuous food source.

3) Bellbirds, tui and all honeyeaters were more abundant in 5 minute bird counts at sites with high intensity of pest control.

Chapter 3: Natural regeneration of *Fuchsia excorticata* seedlings (limitations for recruitment)

3.1 INTRODUCTION

3.1.1 Microsites and environmental conditions

Ecosystem health is often assessed by the ability of a plant community to regenerate (Bassett *et al.* 2005). In order to test for seed limitation in *Fuchsia excorticata*, it is important to determine its preferred natural regeneration conditions first. Four separate components must be recognized in order to define a plant's nich: the habitat niche, the life-form niche, the phenological niche, and the regeneration niche (Grubb 1977). It is well documented in the global literature that regeneration is strongly influenced by light, shade tolerance, herbivory, nutrient availability and gap dynamics.

Forest floors are a mosaic of varying microsites, with varying environmental conditions (Harper 1977, Christie and Armesto 2003). It is considered that co-existence in forests can be largely due to different species having different regeneration niches and responses to light and available microsites (Bellingham and Richardson 2006). The heterogenenous environment that is caused by litterfall on forest floors can set apart a regeneration niche for a given species (Gillman *et al.* 2003).

Leaf litter that decomposes on the soil surface has the potential to intercept light, modify temperature, reduce evaporation of moisture from the soil and release both nutrients and toxic substances into the soil (Fenner and Thompson 2005, p175), consequently inhibiting seed germination and seedling establishment. Within New Zealand, Gillman and Ogden (2005) found variability in regeneration of species under macro and micro litterfall. Macro-litterfall from tree fern species such as *Cyathea dealbata* and *Dicksonia squarrosa*, or cabbage tree (*Cordyline australis*) can damage fragile seedlings when it falls. Canopy cover and associated litterfall can therefore greatly affect microsites for regeneration, and it may be that species that can tolerate large litterfall are of a larger size class, have adapted and selected those sites, and are species that grow up into the canopy and create the large litterfall anyway (Gillman *et*

al. 2003).

F. excorticata seeds are very small (Burrows 1995, Godley and Berry 1995, Webb and Simpson 2001, p260). As leaf litter poses a major barrier to small seeded, light intolerant species (Dupuy and Chazdon 2008), observations of the litterfall environment would prove useful in determining ideal *F. excorticata* regeneration sites.

Soil compaction affects plant recruitment and development due to reduced oxygen availability, increased soil strength and altered water availability (Bassett *et al.* 2005). Highly compact soil can mean seeds are unable to penetrate into the soil profile. Seeds of *F. excorticata* are small, enabling them to infiltrate porous soil easily. Soil compaction also affects root penetration. Fine rooted species have the potential to enter into compacted soil more easily than thick rooted species (Bassett *et al.* 2005).

Other than standard herbivory, non-trophic mammalian damage such as trampling, uprooting by pigs, bark rubbing by deer or bitten but uneaten shoots can have a major but often unrecorded impact on seedling establishment (Wardle *et al.* 2001, Gillman and Ogden 2003). Gillman and Ogden (2003) estimate that 68% of seedlings 10 – 30 cm tall may undergo mortality as a result of non-trophic animal interactions in northern temperate forests in New Zealand. Such mortality of *F. excorticata* seedlings may be an issue in my sites, particularly because they are all within proximity to grassland areas where pests such as rabbits reside, and all have varying densities of possums. Rats (Allen *et al.* 1994, Mulder *et al.* 2009) and slugs (Sessions and Kelly 2002, Joe and Daehler 2008) also have been observed as important seedling predators, and are possibly harming growth of *F. excorticata* seedlings.

Disturbance can improve conditions for seedling recruitment because of increased light and reduced competition for nutrients (Wilson *et al.* 2006). *F. excorticata* is often found colonising light, disturbed sites (Burrows 1995), but has also been observed reinvading areas at Hinewai where gorse has been left to establish (Wilson 1994). The gorse is providing a nurse crop to regenerative bird dispersed plants, as the birds perch on, or fly overtop the gorse, they defecate, dispersing ingested seeds.

The presence of ungulates (sheep *Ovis aries*, goats, deer *Cervus* spp., cattle *Bos Taurus*, King

2005) in regenerating communities can greatly affect the rate and course of establishment of early successional species (Wilson 1994, Wilson *et al.* 2006). Domestic stock (sheep and cattle) are excluded from all four sites and there is no recent record of feral goats at any of them. Ungulate herbivory is likely to be most intense at Mt Thomas where Red Deer was observed (R. Bell *pers obs*). Deer are not known to be present at Hinewai where all ungulates are subject to intensive control, and are actively controlled to low levels at St Arnaud by DOC (Paton *et al.* 2007). Deer are unlikely at the Grampians because of its proximity to the city. So Mt Thomas is the only site likely to be affected by ungulate browse.

3.1.2 Objectives

This chapter aims to answer the following questions:

1) What environmental variables (leaf litter, slope, topography, drainage and canopy cover) are associated with the microsites where *Fuchsia excorticata* seedlings grow?

2) Are any of these environmental variables associated with greater mean seedling height?

3.2 METHODS

In order to find out what environmental variables affect the growth and or height of *F. excorticata* seedlings, random points were compared with points where seedlings were found naturally. Each data point had five variables recorded, which were gained from the 15 cm radius surrounding the chosen point. Leaf litter was recorded as a visual estimate of percentage litter against bare ground per point. Drainage was recorded on a relative scale: good, moderate, or poor. Canopy cover was a visual estimate on a 5 point scale: 1 = <1%, 2 = 1 – 5 %, 3 = 6 – 25%, 4 = 26 – 50%, 5 = 51 – 100%. Slope was measured in degrees with an Abney level and topography was measured by feature (gully, ridge, face, terrace) as per Allen *et al.* (2003). These particular variables were chosen because the impact of these variables on small seeded species (such as *F. excorticata*) has been documented in other species in the literature review.

The same technique was used at all sites; four transect lines of approximately 100 m were walked at each, and the above environmental variables recorded every 5 m, regardless of

whether *F. excorticata* seedlings occurred there or not. Between 20 and 25 data points were collected on each transect line, 100 data points were collected at the Grampians, 90 at Mt Thomas and Hinewai, and 89 at St Arnaud totaling 369 across all four sites., with environmental data for seedlings (and non-seedling locations) recorded along transects.

F. excorticata seedlings were located and measured on 23 July 2009 (n = 5) and 23-24 September 2009 (n = 20) at Hinewai. Seedlings were easier to find in spring when new leaf growth had formed. On 3 September 2009 I searched for *F. excorticata* seedlings at my Mt Thomas site on and around the Red Pine and Wooded Gully tracks (see Figure 2.3). Seedlings were recorded at the Grampians on 1 October 2009 (Figure 2.5) and at St Arnaud (Figure 2.4) on 29 and 30 November 2009 within the general area where focus trees for other experiments are situated.

Attempts to record light availability using a handheld light meter failed at all sites except for Hinewai. These were performed with a LI-COR LI-250 handheld light meter. Those intstrumental measurements of light (recorded as photons in micromoles) at Hinewai correlated strongly and significantly with the visual canopy cover estimates (percentage cover), giving reassurance that the visual canopy cover estimates could be used as an index of the light environment at each spot.

A GLM with binomial error distribution was run in R to test whether selected environmental variables were associated with the presence or absence of *F. excorticata* seedlings, using all microsites. A second analysis was run with gaussian error to see whether any environmental variables were correlated with the height of seedlings. Microsites with no seedling were not included in the height analysis.

3.3 RESULTS

In spring, when fresh leaves were clearly visible, seedlings of *F. excorticata* were found growing at a wide variety of microsites. The Grampians had the most seedlings, with 55 measured. I found and measured 48 at St Arnaud, 38 at Mt Thomas, and 25 at Hinewai for a grand total of 166 seedlings from 369 data points. These ranged in height from 0.5 cm to 181 cm, and had an average height of 20.4 cm. Seedlings grew on the sides of cliffs, on rock

walls, in trackside drains, in creek beds and deep under forest canopy (Figure 3.1). I also measured 203 microsites chosen at random which did not have *F.* seedlings.

Figure 3.1**:** Seedlings growing on a steep stream bank at Mt Thomas (left) and trackside at the Grampians (right) (NB. Not all seedlings visible in this picture are *F. excorticata* seedlings).

Canopy cover and slope were the two environmental variables that were significantly associated with presence or absence of *F. excorticata* seedlings (Table 3.1). Seedlings were more likely to be found in areas with less canopy cover and lower amounts of leaf litter of seedlings (P <0.001 and P = 0.04 respectively). An increase in slope had a positive significant effect on the presence of seedlings (P <0.001, Table 3.1), as did ridges as a topographical measure (P = 0.01). Estimated level of drainage did not have any effect (P=0.07).

Table 3.1a: Analysis of deviance table showing the effect of selected environmental variables on the presence or absence of *F. excorticata* seedlings in a binomial GLM.

Variable	D.F.	Deviance	P(>|Chi|)
Canopy Cover	1	69.9	<0.001
Slope	1	96.14	<0.001
Leaf litter	1	4.37	0.04
Topography	3	11.59	0.01
Drainage	2	5.27	0.07
Residuals	360	320.57	

Table 3.1b: Summary table of binomial GLM testing selected environmental variables on the presence or absence of *F. excorticata* seedlings. (Numbers rounded to three decimal places).

Coefficients	Estimate	Std. Error	Z value	Pr(>|z|)
(Intercept)	2.318	0.743	3.118	0.002
Canopy cover	-1.047	0.143	-7.333	<0.001
Slope	0.069	0.012	5.605	<0.001
Leaflitter	-0.011	0.005	-2.162	0.031
Topography gully	0.234	0.467	0.5	0.617
Topography ridge	1.647	0.515	3.198	0.001
Topography terrace	0.271	0.422	0.643	0.520
Drainage moderate	0.517	0.461	1.121	0.262
Drainage poor	15.233	677.755	0.022	0.982

For seedling height, there was a significant site effect, possibly related to different management histories. The environmental variables were of more interest and most of these had a significant negative association with the height of seedlings (Table 3.2b). Canopy cover is the most significant variable influencing height of seedlings measured in the survey, with dense-canopy areas having shorter seedlings on average (P <0.001, Table 3.2). Increasing slope, poorer drainage, and ridge topography all significantly increased the height of seedlings surveyed (Table 3.2). Interestingly, leaf litter did not show to be affecting the height of *F. excorticata* seedlings (Table 3.2).

Table 3.2a: Analysis of deviance table from a gaussian error GLM testing selected environmental variables against height of naturally occurring *F. excorticata* seedlings.

Variable	D.F.	Deviance	P(> | Chi |)
Site	3	40439	<0.001
Canopy Cover	1	3114	<0.001
Slope	1	794	<0.001
Topography	3	9461	<0.001
Leaf litter	1	28	1
Residuals	156	220450	

Table 3.2b: Summary table from a gaussian error GLM testing selected environmental variables against height of naturally occurring *F. excorticata* seedlings. (Numbers rounded to three decimal places).

Coefficients	Estimate	Std. Error	T value	P (>|t|)
(Intercept)	4.175	0.412	10.128	<0.001
Canopy cover	-0.520	0.072	-7.191	<0.001
Slope	0.014	0.005	2.784	0.005
Leaflitter	-0.003	0.003	-0.956	0.34
Topography gully	-0.026	0.3	-0.087	0.93
Topography ridge	1.437	0.266	5.407	<0.001
Topography terrace	-0.131	0.263	-0.496	0.620
Drainage moderate	0.641	0.248	2.587	0.01
Drainage poor	0.978	0.339	2.889	0.004

3.4 DISCUSSION:

Canopy cover and slope were the most important environmental variables affecting both the presence and growth of *F. excorticata* seedlings in this experiment (Table 3.1, Table 3.2). *F. excorticata* is known to be a colonising species (Chapter 1.4), and is frequently observed growing in disturbed soil. Canopy cover is reduced in slips and disturbances, allowing more light to filter through to the ground, facilitating germination and growth.

The presence of leaf litter affected the chance of finding seedlings of *F. excorticata* in this study (Table 3.1), but it did not affect the height of seedlings when these were present because once seedlings are tall enough to be above the litter layer (a few cm) light availability can no longer kill them. Because litter can intercept light (Fenner and Thompson 2005. p175), it reduces the amount of light available to a seed ready to germinate. *F. excorticata* germination is delayed in dark lab conditions (Burrows 1995). Possibly the main effect of leaf litter is through death of seedlings that have already germinated if a leaf lands on top of them.

Slope explained 30% of the pattern of presence and absence of *F. excorticata* seedlings (Table 3.1), and is likely to be of such great importance to where seedlings are observed because leaf litter cannot accumulate on steep slopes, therefore not intercepting the light that filters through to the seeds. The seeds of *F. excorticata* are so small that they are probably able to

settle on small protrusions, and do not fall down the slope. Slope does not however, affect height of seedlings as dramatically as presence.

Seeing seedlings is not a guarantee of effective regeneration, as these seedlings have a long time to live before they can reproduce, and may die before they get to that age from non-trophic mammalian damage for example. They may also be selfed, and therefore less fit than crossed individuals (Robertson *et al.* 2008, Kelly *et al.* 2010). Apparent high rates of seed set and germination in hermaphrodite plants may be masking an underlying inbreeding problem, and true levels of regeneration should be monitored on the health and abundance of female seedlings (Robertson *et al.* 2008, Kelly *et al.* 2010).

3.5 CONCLUSION

1) Light availability (through varying densities of canopy cover) and slope had the biggest effect on presence of *F. excorticata* seedlings at my sites.

2) Height of seedlings is affected by the slope, canopy cover and ridge topography. Site variation is evident in the height of seedlings, which may be a relic of each site's stage in succession, as well as presence and abundance of ungulates and other herbivores.

CHAPTER 4: *Fuchsia excorticata* in the seed bank

4.1 INTRODUCTION

4.1.1 What is a seed bank?

There is ambiguity surrounding the term "seed bank". Harper (1977) defined it as all the viable (dormant as well as ready to germinate) seeds in the soil of an area, and Roberts (1981) extended this to include all the seeds lying on the soil surface. However, Csontos (2007) states that "seed bank" should theoretically include all potential sources of seeds, such as aquatic or canopy stored seed banks. The definitions by Harper (1977) and Roberts (1981) are sufficient for the purposes in this study, which is technically a "soil seed bank". Often the diversity and proficiency of seeds in a seed bank greatly outnumbers the above ground plant population (Hill *et al.* 2001).

The differentiation between transient and persistent seed banks is most important in the study of seed banks (Csontos and Tamas 2003). Csontos (2007) clarifies some of the limiting factors to seed longevity in the seed bank. A transient seed bank is when any given species' seeds survive for up to 1 year; a short-term persistent seed bank is when seeds survive for 1 – 5 years, and a long-term persistent seed bank is when seeds survive longer than 5 years. Persistent seed banks are an adaptation to fragmented environments and are usually only viable where disturbance is common (Thompson and Grime 1979). In this experiment, the seed bank I refer to hereafter is the soil seed bank.

Dormancy needs some further explanation. Under suitable physical germination conditions a dormant seed will not germinate (Baskin and Baskin 2004). Intensity and physiological patterns of dormancy need to be defined in a study species to determine the life history of a given species (Baskin and Baskin 2004). Burrows (1995) found that the presence of a fleshy pericarp can inhibit germination in many New Zealand woody species, including *F. excorticata.* Burrows used petri dishes in his glasshouse study, which Robertson *et al.* (2006) and Kelly *et al.* (2010) suggest that any inhibiting chemicals present in the fruit pericarp were unable to leach away. In Robertson *et al.* (2006) the whole fleshy fruit did not inhibit the germination of seeds in their in-situ and glasshouse/potting mix trials, as any inhibition effect was able to leach away. These

delays and patterns of germination are evolutionary traits that species have adapted to their environment, allowing them to cope with competition, biotic and climatic hazards, and dispersal.

It is important to learn about soil seed bank dynamics, germination patterns (Spence 1990), seed quantity and spatial and temporal dispersal (Ogden 1985) when wanting to understand the vegetation structure and dynamics. Knowledge gained about the seed banks at the sites in this study will assist in understanding the wider floral community, as well as the specific study species, *F. excorticata.* Seed banks represent the potential of a species to regenerate (Rowarth *et al.* 2007).

4.1.2 *Fuchsia excorticata* in the seed bank

Most New Zealand woody species have no seed bank (Sem and Enright 1996), although there is a tendency for persistent seeds in New Zealand to have smaller seeds (Moles *et al.* 2000). *Fuchsia excorticata* is known to have persistence of seeds in the soil, and it also has little seeds (refer Chapter 1.7). MacDonald (1985) found *F. excorticata* to be present in the seed bank, and deemed it able to germinate upon suitable conditions. At Ahuriri Bush, Port Hills (which I scouted for a potential high fuchsia density site) MacDonald calculated 400 *F. excorticata* seeds per square metre when sifting through soil and counting seeds, and 1211 *F. excorticata* seeds per square metre when counting seedlings germinating from soil samples in glasshouse conditions. Since the seeds of *F. excorticata* are so small, it may be hard to find the seeds in soil samples. MacDonald's second estimate is likely to be a more accurate representation of the quantity *of F. excorticata* seeds in the soil of high density *Fuchsia* forest. Burrows (1994) also classifies *Fuchsia excorticata* as common in Ahuriri Summit.

Germination of *F. excorticata* can happen in 2 – 6 weeks under standard conditions, but can be delayed by up to 8 weeks in dark conditions (Burrows 1995). It is unknown how long *Fuchsia excorticata* seeds persist before dying.

4.1.3 Dispersal away from the parent tree

Fuchsia excorticata may need to disperse fruit further away from a parent tree in order to maximise fitness because they appear to require disturbed sites for recruitment (Robertson *et al.* 2008). However, seeds must encounter suitable microsites in order to germinate and establish. Background numbers of *Fuchsia* in the soil seed bank at distances away from parents will indicate how effective natural dispersal of fruits is. Seed bank analysis combined with seed augmentation experiments (see Chapter 5) can show how much viable seed falls into a habitat suitable for recruitment, and whether it is enough for regeneration of the species.

4.1.4 Objectives

This seed bank experiment helped to determine which species are present but dormant in the seed bank (diversity and abundance); the abundance of *F. excorticata* in the seed bank; the dispersal of *F. excorticata* seeds away from the parent tree; and the effect of parent sex on the number of offspring/seed output. There are very few full seed bank analyses in New Zealand, so counts of all species that germinated in soil in the glasshouse was recorded.

This experiment addresses four main questions:

1) What species are present in the seed bank at the 4 study sites? What are the most common species across all the sites?
2) How does *Fuchsia excorticata* abundance in the seed bank vary with dispersal distance away from a parent tree?
3) Does intensity of pest control (indirectly) lead to an increased abundance of *F. excorticata* seed in the soil seed bank?
4) Does sex of parent tree have any effect on the abundance of *F. excorticata* seeds in the soil seed bank?

4.2 METHODS

4.2.1 Field data collection and set up

In order to determine how abundant *F. excorticata* seeds are in the soil seed bank at each of my sites, a glasshouse experiment was performed. At each of the four study sites (as

described in Chapter 2) 10 mature, reproductive (flowers and/or fruits observed on tree) *F. excorticata* individuals were tagged as replicates. Trees were tagged with flagging tape, sexed (in spring when flowers were present – Table 4.1), and mapped with a GPS (Garmin 60csx) because the same trees were used in the seed augmentation experiment as described in Chapter 5.

Table 4.1: Number and sex of *Fuchsia excorticata* trees at each site.

Site	**Female**	**Hermaphrodite**
Grampians	5	5
Hinewai	4	6
Mt Thomas	7	3
St Arnaud	3	7
TOTAL	19	21

Samples were gathered from St Arnaud and the Grampians between the 2 and 4 December 2008. Mt Thomas samples were collected on the 11 December 2008, and Hinewai samples on the 16 December 2008. Soil was collected at this time of year to ensure that new seeds from the 2008/2009 summer fruit crop were not present in the seed bank, and all seeds would be at least one year old.

At each tree, a measuring tape was laid out 20 m in a randomly chosen direction, so long as the transect lay at least 20 m away from any other *F. excorticata* tree at the 20 m mark. Soil samples were taken at 0 m, 10 m, and 20 m along this transect. A steel soil corer (diameter 63 mm, height 70 mm) was pushed into the topsoil to get a soil volume of 21.82 cm^3 (area = 28.56 cm^2). Four cores were taken at each distance within a 50 cm square (Figure 4.1) and combined to get a larger sample of soil, giving a total volume of approximately 87 cm^3 (area = 85.67 cm^2) of soil per plot. The soil was fastened in a snap lock bag and taken to the University of Canterbury heated glasshouses. Samples were potted up in the glasshouse within 6 days of being collected.

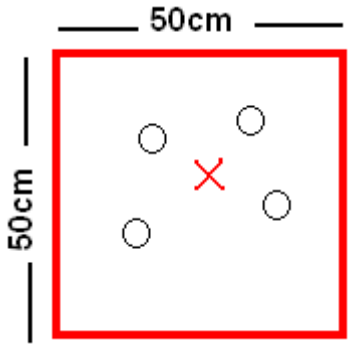


Figure 4.1: Diagram of combined soil samples (four circles) within a 50 cm square at each distance from parent tree.

In summer, the glasshouse was heated to an average of 25 degrees Celsius. In the autumn and winter it would average around 14 degrees because the heating system struggles to regulate the temperature any higher. Reduced watering deterred prevalence of liverworts (*Marchantia* spp.). The liverworts may have excluded light getting through to some seeds, so was picked off. However, *F. excorticata* was also observed pushing through the *Marchantia*.

Each combined soil sample was spread evenly on top of approximately 3 cm of potting mix with slow release fertiliser in a recycled plastic meat tray (23 cm × 30 cm). The soil was spread evenly and clumps of soil were loosely separated by hand to a finer grain soil. In total there were 3 trays of soil per tree (one per distance), which equals 30 trays per site, which over 4 sites is a total of 120 trays in the glasshouse (Figure 4.2). A blank control tray containing plain potting mix was left in the glasshouse to monitor wind-dispersed wilding species that were blown into the glasshouse.

Figure 4.2: Set up of seed trays in glasshouse. The blank control tray can be seen on the far bench in the top left corner of the photograph (Photo: 3/3/2009).

4.2.2 Data collection

From 8 January 2009 any plant that germinated in each of the seed trays was identified and tallied for each tray (Figure 4.3). Care was taken to pull the seedlings out using tweezers, with roots intact. Roots were washed with water over the tray it was removed from to make sure that small seeds remained in the trays. The blank tray had birch seedlings grow, which also came up in some of my seed trays. Birch was removed from the analysis as it was not seen growing naturally at any of the four study sites, but grows naturally nearby the University of Canterbury glasshouses, so it is assumed to be a contaminant.

On 17 June 2009 all seed trays were moved from the glasshouse outside to undergo chilling in natural temperature conditions (Figure 4.4). Chicken wire was laid over top of the trays to prevent birds from digging into the soil, which were probably attracted to worms that had been observed in the trays. Trays were left for 6 weeks, and then returned

to the heated glasshouse on 4th August 2009 to simulate an early spring flush of germination. Over this time, minimum daily temperature ranged between –2.7 and 5.1 degrees Celsius, with an average daily minimum of 1.1 degrees Celsius (Source: Christchurch Botanic Garden, Christchurch City Council and NIWA, Christchurch).

Figure 4.3: Typical growth in seed trays. Left – RNRP #2, 10 m; Right – Hinewai #9, 0 m. (Photo: 3/3/09).

Figure 4.4: Seed trays outside the University of Canterbury glasshouses in the winter.

Trays were then left in the glasshouse for another nine and a half weeks, all seedlings that germinated were counted, and the experiment terminated on 8 October 2009 after 10 months.

4.2.3 Statistical Analysis

Basic statistical descriptors were calculated in Microsoft Excel 2003 on all species to determine general abundance and patterns. Generalised Linear Models (GLM) were run in R (Version 2.7.0) on diversity of species in the seed bank and for *F. excorticata* in particular, using poisson error distribution because data were count data. Number of *F. excorticata* seedlings that germinated per tray was the response variable. Predictor variables were various combinations of site, pest control, distance from parent tree, parent sex and *F. excorticata* density. ANOVA were performed with a Chi test.

The residual deviance (8843.1) was much greater than the residual degrees of freedom (119), which indicates overdispersion. The model was re-run using quasi-poisson distribution to specify more appropriate variance, and without 'site' as a variable to let the model analyse distance, *F. excorticata* density and pest control as factors separately. Interaction factors were insignificant so removed from the model. The minimum adequate model (MAM) results are presented below.

4.3 RESULTS

4.3.1 Species diversity

A total of 74 different species were found in the seed bank of all four sites (Table 4.2). The lowest overall diversity was recorded at St Arnaud (34 species) (Table 4.3). All sites had similar diversity of natives, but some range in the diversity of exotics. The proportion of natives to exotics was about 50:50 at Grampians, Mt Thomas and Hinewai. Of the four sites, St Arnaud had the highest percentage of native species in its total species diversity (Table 4.3). The Grampians was the only site that had more exotic species than native species. There was a significant difference of site on the diversity of species that are present in the seed bank ($P < 0.001$), of the number of exotics in the seed bank ($P < 0.001$) and on the number of natives in the seed bank ($P = 0.01$).

Table 4.2: Full list of species present in the seed bank at each site.

Species name	Common name	Grampians	Hinewai	Mt Thomas	St Arnaud
Acacia melanoxylon	blackwood	√			
Acaena novae-zelandiae	red bidibid		√	√	√
Achillea millefolium	yarrow		√		
Aristotelia serrata	wineberry	√	√	√	
Bellis perennis	bell daisy			√	
Betula pendula	silver birch	√	√	√	√
Blechnum procerum	small kiokio	√	√	√	√
Cardamine hirsuta	bittercress	√	√	√	√
Carex spp.	Sedge	√	√	√	√
Carpodetus serratus	putaputaweta/marbleleaf	√	√	√	√
Carduus tenuiflorus	winged thistle	√			
Centaurium erythraea	centuary	√	√	√	
Cirsium arvense	Californian thistle	√	√		√
Cisium vulgare	Scotch thistle	√	√		√
Clematis vitalba	Old man's beard	√			
Conyza albida	fleabane	√		√	
Coprosma propinqua	mingimingi				√
Coprosma robusta	karamu		√	√	
Cytisus scoparius	broom			√	
Eleaocarpus hookerianus	pokaka				√
Epiliobium ciliatum	willow herb	√		√	√
Epilobium nummulariifolium	creeping willowherb	√	√	√	
Euchiton involucratus		√		√	
Fine forest grass		√		√	
Fuchsia excorticata	tree fuchsia/kotukutuku	√	√	√	√
Gnaphalium uliginosum		√	√	√	√
Grass			√	√	
Hebe divaricata	hebe				√
Hebe salicifolia	koromiko		√	√	
Histiopteris incisa	water fern		√	√	√
Holcus lanatus	Yorkshire fog	√		√	
Hydrocotyle moschata	hairy pennywort	√	√		
Hypolepis ambigua		√	√	√	√
Ilex aquifolium	holly	√			
Impatiens spp.	Busy lizzie	√			
Juncus spp.	rush	√	√	√	√
Kunzea ericoides	kanuka	√	√	√	√
Leptecophylla juniperina subsp. Juniperina	prickly mingimingi			√	
Leycesteria formosa	Himalayan honeysuckle	√	√	√	
Lotus pedunculatus	lotus	√	√	√	√
Melicytus ramiflorus	mahoe	√	√	√	
Metrosideros diffusa	white rata			√	√
Metrosideros fulgans	rata				√
Microsorum pustulatum	hounds tongue		√		
Mimulus moschata	musk		√	√	√
Muehlenbeckia australis	pohuehue	√		√	
Myoporum laetum	ngaio	√			
Paesia scaberula	lace fern				√
Parsonsia heterophylla	New Zealand jasmine		√		

Table 4.2 (cont.) Species name	**Common name**	**Grampians**	**Hinewai**	**Mt Thomas**	**St Arnaud**
Phytolacca octandra	inkweed	√			
Pratia spp.		√			
Prunus vulgaris				√	
Psedopanax arboreus	five-finger	√	√		
Pteridium esculentum	bracken fern	√		√	√
Pteris tremula	shaking brake	√			
Rubus australis	bush lawyer	√	√	√	
Rubus cissoides	bush lawyer			√	
Rubus fruticosus	blackberry	√		√	√
Rumex pulcher	fiddle dock		√		
Schefflera digitata	pate/seven finger	√			
Senecio vulgaris	groundsel	√		√	
Solanum aviculare	poroporo	√			√
Solanum nigrum	black nightshade	√			
Stellaria spp.	chickweed			√	
Taraxacum officianale	dandelion	√	√	√	
Trifolium repens	white clover	√	√	√	
Urtica ferox	tree nettle/ ongaonga	√	√		
Vicia sativa	vetch		√		
Wahlenbergia violacea	violet harebell	√			

Table 4.3: Total species diversity and number of natives and exotic species at each site

Site	**Number of species**	**Natives**	**Exotics**
Grampians	41	18	23
Hinewai	40	21	19
Mt Thomas	42	22	20
St Arnaud	34	20	14

Between each tray in the glasshouse, there was a considerable amount of variance around the median number of species that germinated. Mt Thomas had the largest variance in diversity of species that germinated in one tray, and Hinewai had the smallest spread (Figure 4.5). St Arnaud had the lowest median number of species diversity (Figure 4.5).

A total of 4468 *F. excorticata* seeds germinated into seedlings in the glasshouse across all sites and distances, by far the most abundant seed in the seed bank (Figure 4.6, Table 4.4). An average of 8459 seeds per m^2 were found across all sites. Of the nine most common woody species (other than *Fuchsia excorticata*), abundance of all were significantly different between sites ($P < 0.001$) when tested in quasipoisson GLM's. The nine tested woody species are *Aristotelia serrata* (wineberry), *Carpodetus serratus*

(marbleleaf), *Coprosma robusta*, *Cytisus scoparius* (broom), *Kunzea ericoides* (kanuka), *Leycesteria formosa* (himalayan honeysuckle), *Macropiper excelsum* (kawakawa), *Solanum nigrum* (black nightshade) and *Ulex europaeus* (gorse).

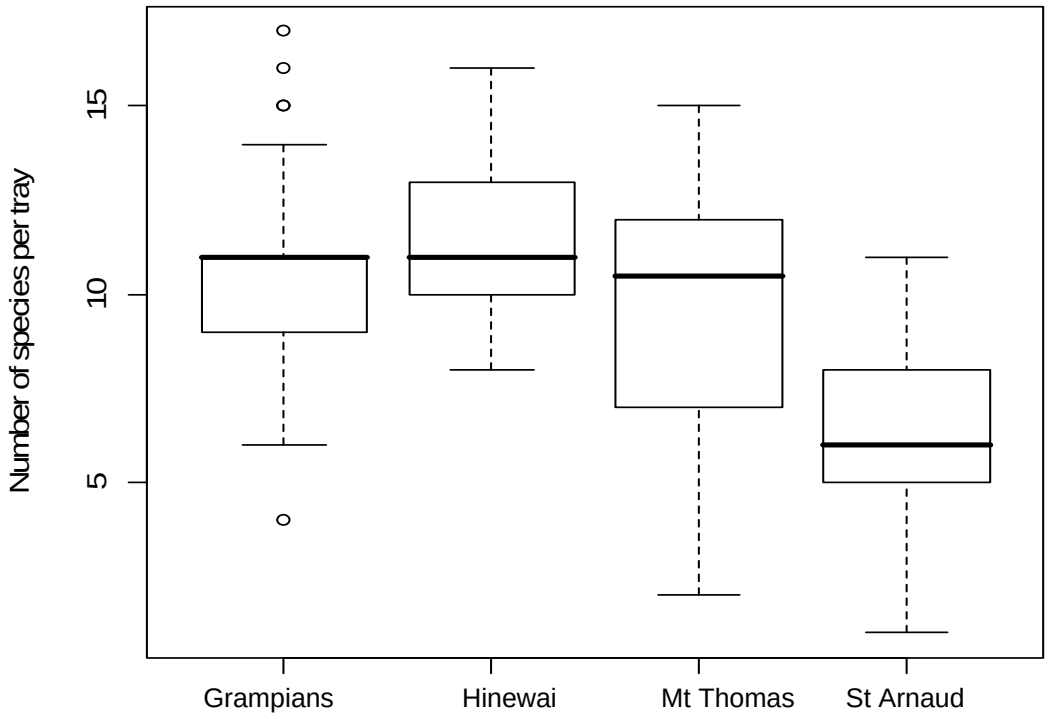


Figure 4.5: Boxplot of number of species that germinated per tray in the glasshouse from each site.

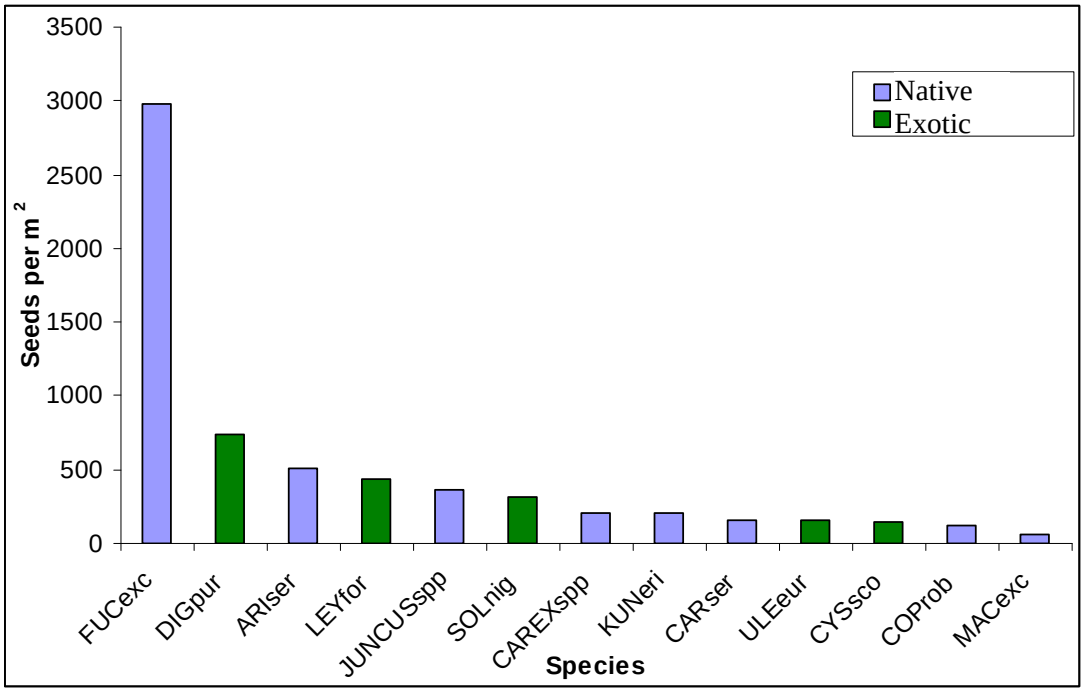


Figure 4.6: Number of individual seeds per m^2 of the 13 most abundant species in the seed bank across all sites. Species in blue are native species and species in green are exotic. Individuals of *Juncus* and *Carex* were identified to genus level. Species names along the x axis follow six letter botanical codes – the first three letters of the genus followed by the first three letters of the species. See Table 4.2 for full names.

Table 4.4: Number of seeds per m^2 of the 13 most common species for each site, and their total number of seeds per m^2 across all sites. Species names follow six letter botanical codes – the first three letters of the genus followed by the first three letters of the species. See Table 4.2 for full names.

Species	**Grampians**	**Hinewai**	**Mt Thomas**	**St Arnaud**	**Total seeds m^2**
FUCexc	461	1190	211	1117	2979
DIGpur	37	652	51	0	740
ARIser	219	209	85	0	513
LEYfor	3	220	214	0	437
Juncus spp	2	143	79	144	368
SOLnig	321	0	0	0	321
Carex spp	23	1	97	90	211
KUNeri	7	194	1	1	203
CARser	17	3	21	121	162
ULEeur	0	79	81	0	159
CYSsco	0	0	141	0	141
COProb	0	3	113	0	116
MACexc	60	0	0	0	60

4.3.2 Abundance of *Fuchsia excorticata* in the seed bank

As shown above (Figure 4.6), *F. excorticata* was by far the most common species present in the seed bank at all sites. Hinewai had the highest median abundance (Table 4.5) of *F. excorticata* seed in the soil seed bank (Figure 4.7). Although St Arnaud had a high mean number of seeds, the median is much lower (Table 4.5, Figure 4.7), which is resultant from the few high outliers. Grampians and Mt Thomas both had mean and median values which wrap more closely around each other. The abundance of *F. excorticata* seed in the seed bank is significantly different between sites (P = 0.002).

Table 4.5: Mean and median numbers (per tray) and average per m^2 of *F. excorticata* seeds in the seed bank by site.

Site	Mean	Median	Seeds per m^2
Grampians	23.1	18	461
St Arnaud	55.8	8	1117
Mt Thomas	10.5	4.5	211
Hinewai	59.5	48	1190

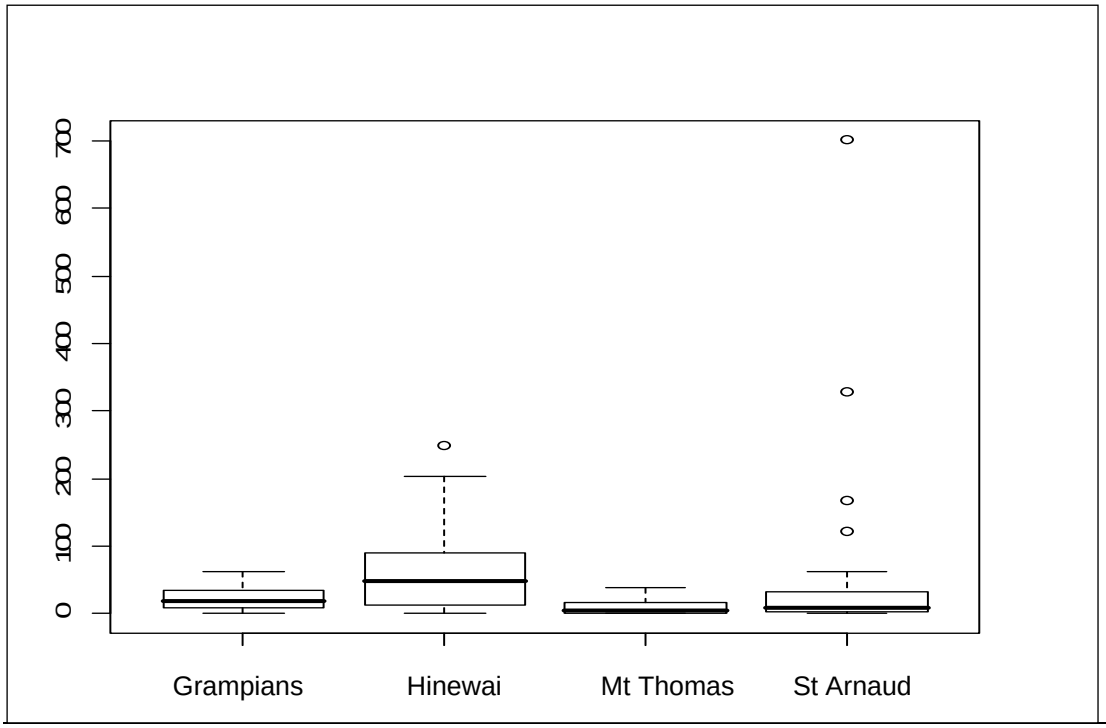


Figure 4.7: Boxplot showing upper limit, upper quartile, median (bold line), lower quartile and lower limit of *Fuchsia excorticata* seed in the seed bank at each site.

4.3.3 Does *Fuchsia excorticata* abundance in the seed bank vary with dispersal distance away from the parent tree?

Abundance of *F. excorticata* seed in the soil declined with dispersal distance away from the parent tree at all four sites. St Arnaud had the biggest decrease in seed abundance across distance, with over 95% reduction in seeds (Table 4.6, Figure 4.8). However, St Arnaud had more than twice as many seeds per m^2 at 0 m as the next most abundant 0 m seed bank, (Hinewai). Hinewai had the most uniform seed bank across dispersal distance, with nearly 85% of seeds remaining per m^2 at 20 m that were present at 0 m. Hinewai even had an increase in seed abundance between 10 m and 20 m. Mt Thomas remained the lowest seed bank at all distances. Although Grampians seed abundance declined steadily with increasing distance, it retained 43.6% of seeds at 20 m, which was the second highest across distances.

Table 4.6: Mean number of *F. excorticata* seedlings that germinated in the glasshouse at each site and at each distance from the parent tree showing decline across distance.

Distance	**Grampians**	**Hinewai**	**Mt Thomas**	**St Arnaud**
0	34.2	68.2	21.1	150.2
10	20.1	52.7	7.1	10.4
20	14.9	57.6	3.4	6.9
% of FUCexc from 0m at 20 m	43.6	84.5	16.1	4.6

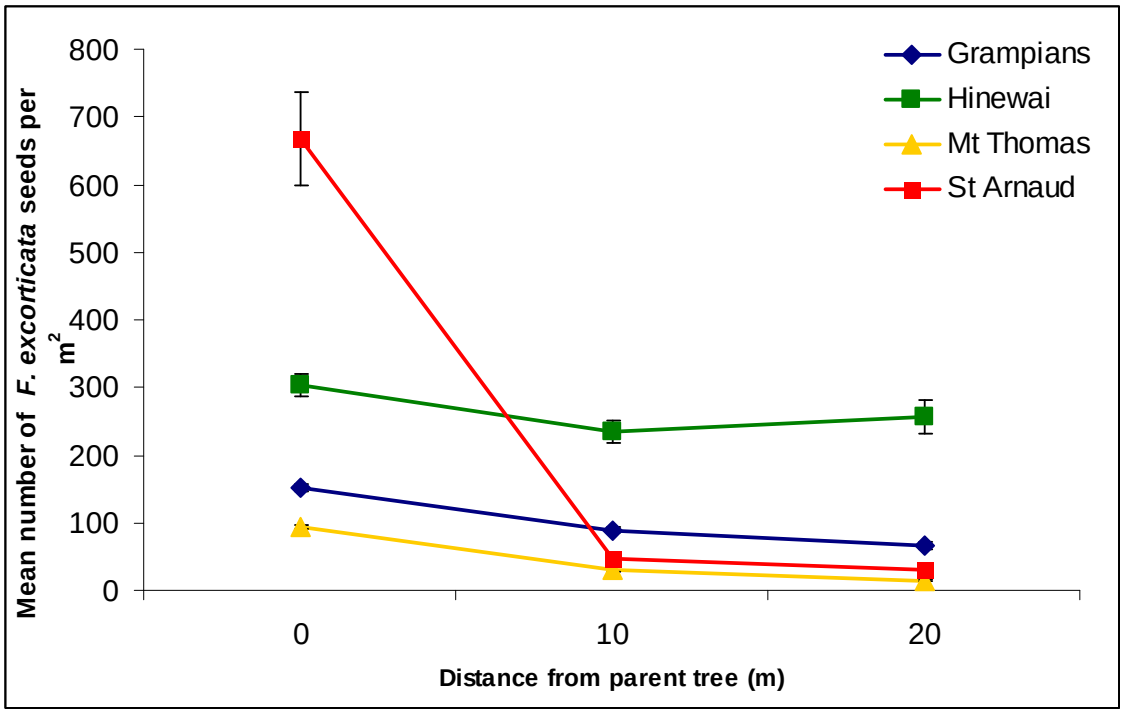


Figure 4.8: Mean abundance of *F. excorticata* seed in the soil seed bank per m^2 across dispersal distance away from a parent tree at each site.

4.3.4 Pest control

Intensive pest control occurs at Hinewai and St Arnaud, and intermittent pest control occurs at the Grampians and Mt Thomas. The seed bank was significantly higher ($P < 0.001$) at sites where intensive pest control is occurring than sites with low pest control. Seed bank abundance per m^2 decreased significantly ($P < 0.001$) across distance away from the parent tree, but there was no interaction effect between distance and pest control ($P = 0.7$) (Table 4.7, Figure 4.9).

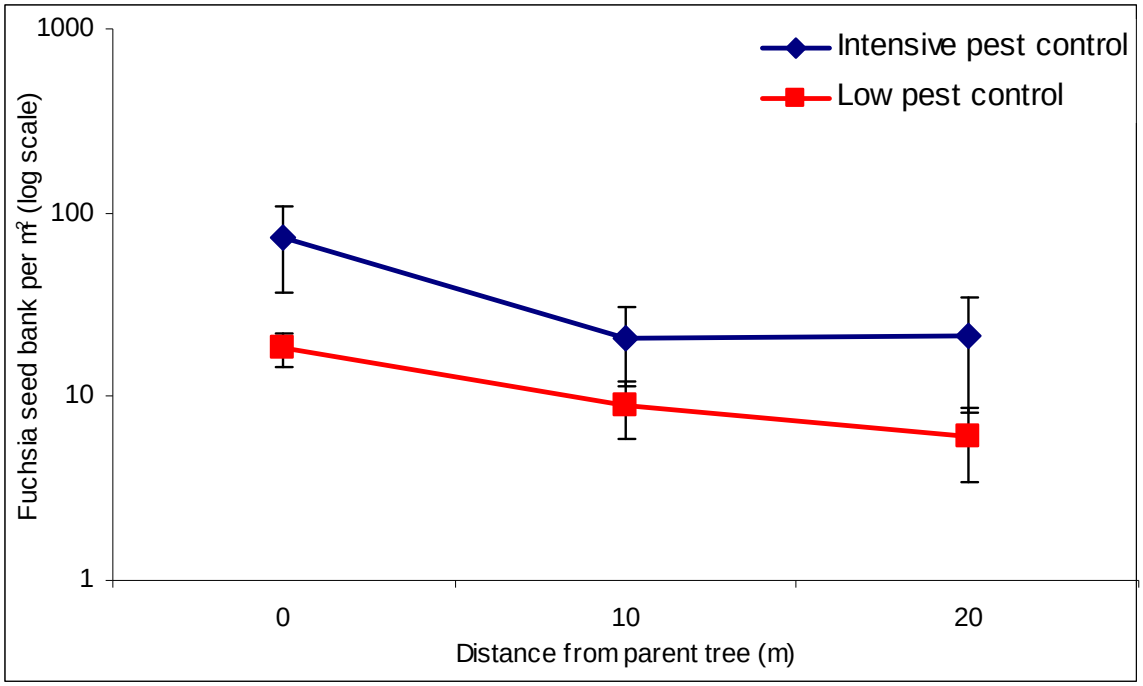


Figure 4.9: Mean abundance of *F. excorticata* seeds in the seed bank in relation to intensity of pest control. Intensive pest control sites are St Arnaud and Hinewai; and low pest control sites are Grampians and Mt Thomas.

Table 4.7: Analysis of variance table testing abundance of *Fuchsia* seed in the seed bank against distance, site, pest control intensity and the interaction effect between distance and pest control. High intensive pest control sites are Hinewai and St Arnaud, and low intensive pest control sites are Mt Thomas and the Grampians. Statistical results are from quasipoisson GLMs

	Df	Deviance	P(>|Chi|)
Distance	1	1269.0	<0.001
Pest control	1	1422.9	<0.001
Site	3	1570.1	0.002
Sex	1	733.6	0.016
Distance × Pest control	1	8.7	0.7
Residuals	115	6089.5	

When the GLM is run without "pest control" as a factor, site and the interaction effect of "distance × site" became highly significant (Table 4.8). There was a significant difference in the abundance of *Fuchsia* seed in the seed bank between sites, and across distance.

Table 4.8: Analysis of variance table testing abundance of *Fuchsia* seed in the seed bank against distance and site, and the interaction effect between distance and site. Statistical results are from quasipoisson GLMs

	Df	Deviance	P(>|Chi|)
Distance	1	1269	<0.001
Site	3	1570.1	<0.001
Distance × site	3	1215.1	<0.001
Residuals	112	4788.9	

4.3.5 Hermaphrodites and female parent trees affect seed set

The sex of parent *F. excorticata* tree has a significant effect on the number of *F. excorticata* seeds in the seed bank (P = 0.0164). More *Fuchsia* seed is produced by hermaphrodite parent trees than female parent trees. Females have on average 14 seeds per m^2, and hermaphrodites have 34. Over distance hermaphrodite parent trees maintain a higher mean abundance of seed than females at all distances away from the parent tree (Figure 4.10).

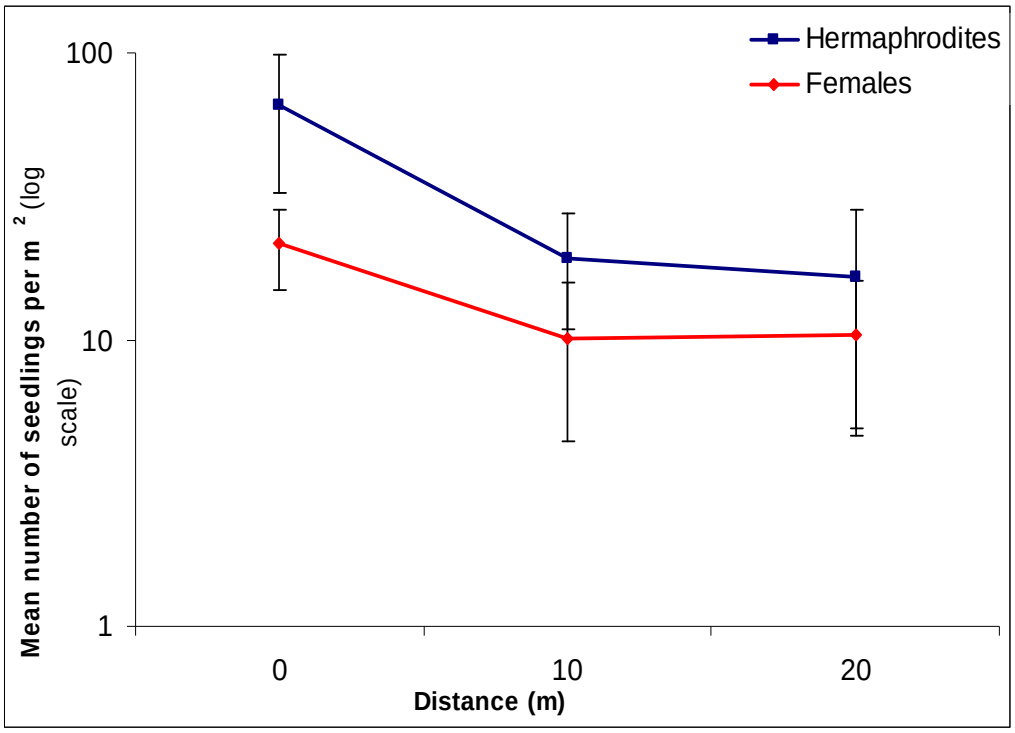


Figure 4.10: Mean number of *Fuchsia excorticata* seedlings per m^2 across distance dependent on sex of parent trees.

4.4 DISCUSSION

4.4.1 Species diversity of the seed bank

The sites in this study (Table 4.1) are slightly less diverse than the seed bank study completed at Karori Wildlife Sanctuary in 1999, where 46 species were found to germinate (a total of 1736 seedlings, Moles and Drake 1999). However, I had a total of 12 688 germinants across my 120 samples, and a total diversity of 74 species across all sites.

Enright and Cameron (1988) found strong evidence for the invasion of the soil seed bank by adventive weedy species at Huapai. Common roadside and pasture weeds are easily wind and animal dispersed, so the closer a site is to roads and adjacent farmland, the more likely it is to accumulate adventive seeds (Taylor 1980). The lowest species diversity at St Arnaud and highest species diversity at Mt Thomas shows the differing prevalence of invasive weedy exotic species. Exotic species recorded include invasive grasses and herbaceous species, and then some woody species such as broom, gorse and Himalayan honeysuckle in the understory. The upper canopy is dominated by beech (Mt Thomas and St Arnaud) or primary and secondary successional native broadleaved species such as mahoe, tree fuchsia, wineberry and five-finger (Hinewai and Grampians).

Seeds from *Juncus* spp. have been thought in the past to be transported via water movement in the soil at some sites (Partridge 1989). The largest count of *Juncus* spp. seeds (105) was at a Hinewai 0 m plot, which, incidentally is on a stream bank, increasing the likelihood of water borne dispersal.

It is important to know that estimates of seeds per metre square are likely to have a high variability because of the small ground area actually sampled, and the probable spatial variation in seed bank characteristics (Enright and Cameron 1988). Nonetheless, they can be compared to one another. A total of 8459 seeds m^{-2} were found in the seed bank across all sites, which is similar to the number of seeds (8841 seeds m^{-2}) in the seed bank in a *Pinus radiata* plantation before restoration into native bush at Karori Wildlife Sanctuary (Moles and Drake 1999). Between 134 and 5388 seeds m^{-2} (Sem and Enright 1996) and 1131 seeds m^{-2} (Enright and Cameron 1988) have been found in kauri (*Agathis australis*) forests and 500 – 3000 seeds m^{-2} in North Island shrubland forest (Ogden 1985). Herbert

(1976) obtained between 50 – 1000 native species seeds' per m^{-2} in Pureora and Tihoi state forests in the North Island. Over 8000 seeds m^{-2} appears to be an extremely high seed bank occurring across all sites in this study when compared with other New Zealand seed bank records.

Weedy species are entering canopy gaps and opportunistic, well lit and disturbed sites. However, species that can establish under low light conditions are more likely to provide a threat to restoration and native species than species such as foxglove which require high intensity of light (Moles and Drake 1999). St Arnaud is a more mature and later stage of succession forest, with a tall established *Nothofagus* canopy. Older forests tend to have lower density seed banks (Thompson 1978, Sem and Enright 1996), as early successional species lose viability. The study area is in the Nelson Lakes National Park so is therefore relatively undisturbed, which is probably why it is showing fewer exotic species in the seed bank and a lower overall diversity. In this scenario, it is important to look at overall community composition, and what species dominate, not just at overall diversity which can give a false sense of the health of the forest community.

Alien species often have persistent seed banks, and are able to establish greater densities in the seed bank than in the seed rain (Holm *et al.* 1977, Drake 1998). Knowledge gained about the alien species present in the seed bank can help managers in determining strategies for control (Moles and Drake 1999). The Grampians, Hinewai and Mt Thomas all have gaps of forest where woody weed species have once been dominant, but are slowly but surely being encroached upon by secondary succession species. Once overtopped, seeds of species such as gorse and broom are unlikely to germinate as microsite conditions may be unsuitable due to lack of light or soil moisture, even though they remain in the seed bank for a very long time (Hill *et al.* 2001). For instance, even without nearby *Ulex europaeus* plants, there was a deeply buried seed bank of 6500 seeds m^{-2} on the Port Hills (Partridge 1989). Unlike Sem and Enright's (1996) prediction, this study confirms that several native New Zealand woody species do display some dormancy and have a seed bank.

4.4.2 Overall abundance of *Fuchsia excorticata* seed in the seed bank

F. excorticata was once thought to maintain small seed banks of 10 -100 seeds per m^2 in forest areas (Ogden 1985). This study contrasts Ogden's statement, with records over 1000 seeds per m^2 in two sites (Table 4.3). Burrows (1997b) states that *F. excorticata* seed exhibits some degree of primary dormancy, as it can withstand drying despite its small size, and can still germinate at least 2 years after seed set. It also displays pre-dispersal seed storage, as fruit and flowers can often been seen on the same tree at the same time, and fruiting occurs over an extended period of time (Burrows 1997a). The seeds that germinated in the glasshouse in this experiment are at least 9 months old (from the 2008 fruit crop) because soil samples were collected in December 2008, before the 2009 fruit crop had set. Conditions for germination only became adequate when the seeds entered the glasshouse. The largest overall seed bank out of the four sites is found at Hinewai, where there is a high density of *Fuchsia excorticata* parent trees and a high intensity of pest control (see below 4.4.4). As *F. excorticata* is known to have germination over 90% (Burrows 1994), these results are likely to be a true indication of the numbers of seeds present in the seed bank.

Ogden (1985) suggests that 10 – 600 viable seeds per m^2 are required to maintain a forest or shrub community, and less than 100 seeds per m^2 should be sufficient given appropriate microclimates. *F. excorticata* is found in the seed bank at Karori in densities of 535.7 seeds per m^2, which sits about the middle of the densities found at the sites in this study (Table 4.3). Interestingly the Karori figure is higher than densities at Mt Thomas and the Grampians, (the two low pest control sites), even though there was no seedling, sapling or adult *F. excorticata* recorded in vegetation surveys at Karori at the same time.

F. excorticata seed has been found in sub-montane seed banks (Martin and Ogden 2002), and has also been found in the seed bank at grassland sites adjacent to forest scrub on the Banks Peninsula (Partridge 1989); indicating it is able to be dispersed to other sites away from parent trees, and into a variety of habitats, or, its seed remains in the seed bank from a prior vegetation state which has been removed or destroyed by fire.

4.4.3 The effectiveness of the *Fuchsia excorticata* seed dispersal service

Regional differences in frugivore behaviour, diversity and abundance are known to be a major influential factor in seed dispersal, seedling establishment and spatial distribution of seedlings and trees (Bleher and Bohning-Gaese 2001). The site difference in abundance of effective seed dispersers, as well as density and abundance of mature fruit-bearing trees is likely to be leading to an inconsistent dispersal service of *Fuchsia excorticata* seed away from parent trees at the different sites in this study.

It is often hard to distinguish whether size and composition of a seed bank are resultant from the current mature vegetation, a past vegetation community, or are arriving from long-distance dispersal (Ferguson and Drake 1999). Ogden (1985) also states that *F. excorticata* has long lived seeds, because seedlings appear in soil samples long distances away from living parent trees, and where adults have been destroyed because of herbivory. Ferguson and Drake (1999) found major disparities in abundance of bird dispersed seeds between forest (3742 seeds per m^2) and grassland (7.7 seeds per m^2).

Partridge (1989) found *F. excorticata* to be a major contributor to the seed bank, even at greater dispersal distances at their study on the Port Hills. Hinewai is the only site with a high density of *Fuchsia excorticata* and a high intensity of pest control, which means there is a likely increased abundance of avian pollinators. The high abundance of bellbirds at Hinewai effectively pollinate the flowers and disperse the fruit. The higher seed set as a result of the improved pollination is evident in the higher seed bank. Dispersal of nearly 85% of the seed to 20 m from the parent tree indicates the birds are performing an efficient dispersal service, and seed is being spread to more sites, meaning any given seed has an increased chance of finding a suitable site for regeneration.

At the three other sites however, the percentage of seeds that are present at 20 m is less than half of that present at 0 m, indicating a poorer dispersal service of seeds into potential suitable germination and/or establishment sites. The Grampians is likely to have the second highest abundance of *F. excorticata* seed in the seed bank across distance because of its high density of very large adult *F. excorticata* trees. Tui and bellbird are present at the Grampians in moderate numbers, and are attracted to the fleshy fruit, and seem to be providing an adequate seed dispersal service.

The lack of pest control at Mt Thomas has meant bird numbers are low and the dispersal service away from parent trees appears to have suffered as a result. Pollination is likely to be reduced as well, which is evident in the modest number of *F. excorticata* seeds at 0 m along the dispersal transect.

Fleshy fruited species have previously been observed to drop maximal seed rain beneath parent trees (Traveset *et al.* 2003) because frugivores perch on their chosen food source for long periods of time, and because undispersed fruit falls to the ground beneath the parent tree when overripe. *F. excorticata* is exhibiting this pattern at all sites, but particularly at St Arnaud (Figure 4.8). The high density of tui and bellbirds at St Arnaud resultant of the intensive pest trapping in the Rotoiti Nature Recovery Project (RNRP) (Chapter 2) is expected to improve the pollination service of *Fuchsia excorticata*, and therefore seed set. Any undispersed fruit is likely to fall straight to the ground beneath parent fuchsia trees (Kelly *et al.* 2010).

However, seed abundance drops down rapidly at 10 m and 20 m at St Arnaud. *F. excorticata* is not very common at St Arnaud, with a few small trees dotted in the understory, and seedlings and saplings colonising disturbed or wet sites in streambeds. A handful of larger trees are present in the stream at the head of Kerr Bay. The fact that it makes up only a tiny portion of the biomass, and fruit that is consumed and dispersed elsewhere is such a minor portion of the diet of frugivorous birds at St Arnaud, plentiful dispersal of seeds far away is reduced.

4.4.4 Ecosystem-wide effects of invasive species

Pollinator behaviour and characteristics are influenced by the abiotic environment, and also the distribution and characteristics of plants, which reflect seed number and quality (Nathan and Muller-Landau 2000). At sites where pest control is more intensive, bird numbers should theoretically increase. Bellbird nest survival and densities increased significantly after intensive stoat trapping at Craigieburn (Kelly *et al.* 2005). Higher abundance of tui and bellbirds should result in an improved pollination and dispersal service, and therefore an ensuing larger seed set and more opportunities to find safe sites for germination. Intensive pest control sites are supporting this theory, with significantly

higher abundance of *Fuchsia excorticata* seed in the soil than sites with low intensity of pest control (Table 4.7, Figure 4.9).

At Hinewai and St Arnaud, intensive trapping for possums (and mustelids at St Arnaud) as part of the reserve management regime lead to visibly and aurally more numbers of bellbirds, (and tui at St Arnaud). Thirty tui were released at Hinewai in April 2009, and were nesting this spring/summer (2009/2010) breeding season (H. Wilson *pers. comm.* 2009). It will be interesting to see how well tui establish at Hinewai with an already abundant bellbird population, and whether their re-introduction to Banks Peninsula benefits the pollination and health of *F. excorticata* and other mutually dependent plants.

"Birdlife on the Grampians", a community group formed from within the Nelson branch of the Forest and Bird Society set up pest trap lines in October 2009 targeting possums, mustelids and rodents in the Grampians Reserve. It will be interesting to see what the introduction of pest control to the reserve does to the abundant *F. excorticata* population there, as the trees are very mature and seedling regeneration appears to be successful in the disturbed areas.

Traditionally, stitchbird would have provided *Fuchsia excorticata* with pollination and dispersal services in North Island forests (Chapter 1), as they are notably attracted to *F. excorticata,* but it's extinction from the mainland has made it "functionally extinct" (as per Sekercioglu *et al.* 2004). The silvereye arrived naturally from Australia circa 1850 and has established an abundant and important population nationwide, performing 31% of native flower visits (Kelly *et al.* 2006). It is possible that the silvereye has replaced much of the ecosystem services that would have originally been performed by stitchbird.

However, silvereyes are known to nectar-rob hermaphrodite flowers (Robertson *et al.* 2008). The floral tube is too long for a silvereye's beak to penetrate the nectar of a hermaphrodite flower, whereas the shorter female floral tube enables silvereyes to collect nectar and transport pollen onto the stigma and perform an effective pollination service. However, robbing rates vary seasonally and spatially, and there is no correlation between robbing rates and silvereye visitation (Robertson *et al.* 2008). Silvereyes were present in high numbers and observed visiting *F. excorticata* trees only at Hinewai.

4.4.5 Gynodioecy

Pollen limitation of flowers is defined as the subsequent reduction in seed set in the fruit (Ashman *et al.* 2004). In gynodioecious *Fuchsia excorticata*, hermaphrodite trees in a range of North Island and South Island sites had lower mean pollination limitation indices (0.17) than female (0.40), which means that 17% and 40% of seeds respectively that would have ripened did not because of insufficient pollen receipt (Robertson *et al.* 2008). The pollen limitation that *Fuchsia excorticata* is experiencing due to reduced bird densities (and hence reduced visits to flowers,) throughout much of mainland New Zealand reduces the seed set, and the results presented here (Table 4.7, Figure 4.10) now give further evidence as to the consequences of pollination limitation; the disparity between seed banks of female and hermaphrodite parent trees.

However, the fact that hermaphrodites can autonomously self may mean that some seeds are inbred, and therefore may be worth less to regeneration, especially if they don't survive to reproductive age (Scofield and Schultz 2006). Although parent hermaphrodite trees are able to produce more seed, this may be a false reproductive assurance as the relative fitness of seed is likely to be poorer because of inbreeding depression (Robertson *et al.* 2008), leading to further regeneration failure.

Furthermore, pollinator behaviour may affect the chance of inbreeding. Craig (1989) observed tui on *Phormium tenax*, noting that most birds move between flowers on the same plant, increasing the likelihood of geitonogamous pollen deposition. The bird observations performed in this thesis (Chapter 2), confirm that the same was often true of bellbirds, tui and silvereye on *F. excorticata* trees, particularly if they are prolific flowerers (R.Bell *pers. obs*.).

Female flowers must receive pollen from hermaphrodites so are always outcrossed, and because they are smaller and produce less nectar than hermaphrodites, they are likely to be less attractive to pollinating visitors (Delph and Lively 1985, Robertson *et al.* 2008). At Mt Thomas, seven out of the ten trees where seed bank measurements were taken were female (Table 4.6), and it is the site that exhibited the smallest output of seeds (Figure 4.8). These results suggest that the females were more likely to be seed limited as their overall seed bank production was stunted from the pollination limitation.

4.5 CONCLUSIONS

The following conclusions can be made from this experiment:

1) The overall seed bank displayed at the study sites is less diverse than other records, however is more abundant. Prominence of native and exotic species varies between sites, depending on age of stand and surrounding vegetation.
2) The *F. excorticata* seed bank at each site has shown to be persistent and showed similar numbers to other records of *F. excorticata* in New Zealand.
3) Dispersal of *F. excorticata* seed away from a parent tree is increased in sites where it is more abundant, and therefore a more prominent food source.
4) Higher intensity of pest control increases the abundance of *F. excorticata* seed in the seed bank as a result of a suspected improved pollination service.
5) The stronger pollination limitation experienced by *F. excorticata* females (Robertson *et al.* 2008) is evident in the seed bank, as hermaphrodite parents have higher numbers of seeds in their seed banks than females.

The most important conclusion that can be made is the ecosystem-wide effect of pest control, which is likely to lead to an increased number of birds that are able to pollinate the ornithophilous *F. excorticata* flowers. An improved pollination service brings an increased seed set, which was evident in the seed bank. Dispersal of fruit to increased distances from a parent tree was higher at sites with high densities of *F. excorticata* (the Grampians and Hinewai), but highest at Hinewai, where there is a high density of parent trees combined with intensive pest control, and therefore increased bird densities. This seed bank analysis verifies the ecosystem-wide effects and benefits of pest control.

Chapter 5: In situ seed sowing

5.1 INTRODUCTION

5.1.1 Seed sowing within the *Fuchsia excorticata* ecological community context

To determine what limits plant population abundances and distribution, studies must be carried out to understand the principal ecological mechanisms operating in the target community. Two opposing views dominate the understanding of these mechanisms: the availability of suitable microsites (establishment limitation), and the availability of seeds (seed limitation). The prognosis is confounded by the fact that the two views are often assumed to be mutually exclusive (Clark *et al.* 2007). Calvino-Cancela (2007) found both seed and microsite limitation in the shrub *Corema album*, dependent on whether recruitment occurred in open grassland or beneath other trees. Seed sowing experiments could be used to reveal information about community structure (Turnbull *et al.* 2000), and are seen as the only reliable evidence to determine seed, habitat, dispersal, microsite and recruitment limitation (Munzbergova and Herben 2005).

Herbivore exclosure cages can be used to distinguish the effects of predators on seedling establishment (Wilson *et al.* 2003). However, seed predation is only likely to be of any significance to plant recruitment if the species is seed limited, and if so, the impact of seed and/or seedling predation will be reduced or exacerbated according to the severity of the seed limitation (Calvino-Cancela 2007). Seed predators have no effect on plant population density if they consume seeds that were doomed to die because of landing in unsuitable microsites or in areas with high densities of conspecific seeds.

5.1.2 Seed sowing experiments – a background

Turnbull *et al.* (2000) reviewed seed augmentation and seed introduction experiments that were used to determine seed limitation in a range of species. Seed augmentation is the seed addition of species' that are already residents of the target community. It can be

assumed with already resident species that their regeneration niche exists/existed in that target community, and recruitment is not restricted by environmental conditions. In seed introduction, the sown species do not naturally occur within the target community. Absence may be due to unsuitable regeneration conditions, in which case recruitment will not occur regardless of how many seeds are added into the soil, or their relative densities. Alternatively, historical accidents may mean that a species has not arrived at a site, even if conditions are suitable for a population to establish.

Table 5.1: Limitation conclusions from sowing experiments concerning recruitment in plant populations. (Adapted from: Eriksson and Ehrlen 1992) NB. Conclusions A, B and C are not mutually exclusive.

TREATMENTS US = Undisturbed, seeds added UC = Undisturbed, control DS = Disturbed, seeds added DV = Disturbed, control	
OBSERVATION	CONCLUSION
A. If US>UC and/or DS>DC	Seed limitation
B. If DS>US and/or DC>UC	Microsite limitation
C. If DS>US and DS>DC	Seed and microsite limitation
D. If US = DS = Controls	Either 1.) Uninformative or 2.) No seed limitation

5.1.3 The effect of seed size on establishment

An inverse relationship occurs between the numbers of seeds a plant can produce for a given amount of energy, and the mean mass of the individual seeds produced (Smith and Fretwell 1974, Henery and Westoby 2001). Seed mass is an important part of the life history strategy of a plant species (Moles and Westoby 2002), so knowing the seed mass of a species can help predict its response to seed supplementation, as species with larger seeds are more likely to show increased recruitment in seed addition experiments. Small seeds are more susceptible to environmental stresses, such as drought, shade and

competition. The lower abundance of large seeds is thought to be compensated for at the establishment phase, as large seeds are more likely to survive adverse conditions (Moles and Westoby 2002). Seed mass can promote germination in seed addition experiments, as larger seeds invest more into the cotyledon stage that occurs after germination (Moles and Westoby 2002). Because seed output of small seeds is relatively high, often small seeds are limited by patch availability, as opposed to the seed availability constraints that large seeds face.

Fuchsia excorticata has small seeds (0.06 mg) (Moles *et al.* 2000), so is therefore likely to show less evident signs of increased recruitment following addition (Moles and Westoby 2002). This may indicate microsite limitation rather than seed limitation (Table 5.1). Seed addition at differing densities can help determine whereabouts on the seed-microsite limitation gradient a particular species' population lies (Moles *et al.* 2002).

Because *F. excorticata* has small seeds, and persists for a long time in the soil, the seeds are exposed for long periods of time to burrowing seed predators and fungal pathogens (Moles and Westoby 2006). Conversely, the fact that *F. excorticata* has a seed bank (MacDonald 1985, Bartholomew 2008, Chapter 4 – this thesis) shows that seeds probably survive predation because of their small size, and also makes it less likely to suffer from seed limitation.

5.1.4 Objectives

This chapter aims to determine whether *F. excorticata* seed abundance and distribution is limited by microsite availability (establishment) or by seed availability (seed limitation), specifically:

1) Will addition of *Fuchsia excorticata* seeds onto soil where *F. excorticata* is already present produce more seedlings than plots where seed is not added?
2) Will plots with herbivore exclosure cages protect seedlings from herbivory, resulting in more seedlings than plots without cages?
3) Is there stronger evidence for seed limitation at greater distances away from the parent tree in sown plots?

5.2 METHODS

5.2.1 Location and layout

Seed addition experiments were conducted at the same sites where soil was collected for the seed bank analysis (Chapter 4). At each of the four study sites, 10 mature reproductive *F. excorticata* trees were marked and tagged, with a 20 m transect laid in a random direction, so long as it was away from other *F. excorticata* trees. Plots were marked at 0 m, 10 m and 20 m along each transect (Figure 5.1). Therefore the 20 m plot was at least 20 m from its marked tree, as well as any other reproductive *F. excorticata* tree.

Seed augmentation experiments were set up in late summer when local *F. excorticata* fruit were ripe so seed could be collected for sowing. Mt Thomas fruit were ripe first, so experiments were set up on 15 and 19 January 2009. At the Grampians, experiments were set up on 7 February 2009; at St Arnaud on 8 and 9 February 2009; and at Hinewai (which has a later fruiting season probably due to latitude and elevation) on 6 and 7 March 2009.

5.2.2 Slurry

F. excorticata fruits have around 266 ± 92 seeds encapsulated in a fleshy fruit (konini) (Burrows 1995). In order to add seed into plots, 5 ripe *F. excorticata* fruits were mashed up with a butter knife to loosen the seed and mixed with tap water into a slurry containing ~1300 seeds. The slurry was prepared in a plastic vial with a volume of approximately 28 ml. *F. excorticata* fruits that were used in the slurries were collected from numerous trees in the same or nearby locations to the target trees used in the study, ensuring that fruit was not collected from the marked target trees. This technique was used to conserve time with counting out a specific number of seeds, and to guarantee enough viable seeds would be included.

In Nelson at the Grampians, the majority of fruiting *F. excorticata* trees are large (up to 12 m tall), so fruit was inaccessible. *F. excorticata* fruit was therefore gathered from the

Brook Waimarama Sanctuary (Figure 2.5), which is located 2.5 km to the south east of my Grampians site (within flying distance for avian dispersers). At St Arnaud, fruit was collected from individual trees on the western edge of Lake Rotoiti, and from a few unmarked individuals within the study area. Because the RNRP is a low density *F. excorticata* area, fruit was scarce, and only able to be gathered from about 5 trees.

Both of the Canterbury sites had enough mature *F. excorticata* to be able to collect a mixed array of fruits from within the wider study area. At Hinewai fruit was collected from the abundant fruiting trees on the East Track and the Wahanu Track (Appendix 1). At Mt Thomas fruit was collected from trees on the Red Pine and Ridge track at the Wooded Gully entrance to the forest park.

I placed 100 seeds from a selection of the sample fruit on filter paper in petri dishes in the laboratory in Christchurch to test seed viability. All provenances had viable seeds (Hinewai – 14%, St Arnaud – 64%, Grampians – 14%, Mt Thomas – 45%).

5.2.3 Cages

Herbivore exclusion cages were placed on two of the four plots at each plot distance to determine whether herbivores had an effect on the germination and/or survival of *F. excorticata* seedlings. Circular cages were made from a 30 cm x 61 cm rectangle of 5 mm grid welded mouse-proof mesh wire (see Figure 5.2a). Cages were fastened in place with two pegs made from 10-gauge wire.

To mark the two control plots without herbivore exclusion cages, a 61cm length of fine lacing wire was cut and formed into a circle (with the same circumference as the cages), which was secured to the soil with fine wire pegs (Figure 5.2b.). The loop was open, which meant herbivores had free access to the plot. These are referred to as the “non-caged” plots.

At each plot distance there were two caged and two non-caged plots randomly placed around the measured distance (Figure 5.1, Figure 5.2a.). One of the caged and one of the non-caged plots had seed added by washing the slurries out of the vials with a drink bottle (Figure 5.3). The other caged and non-caged plots did not have seed added.

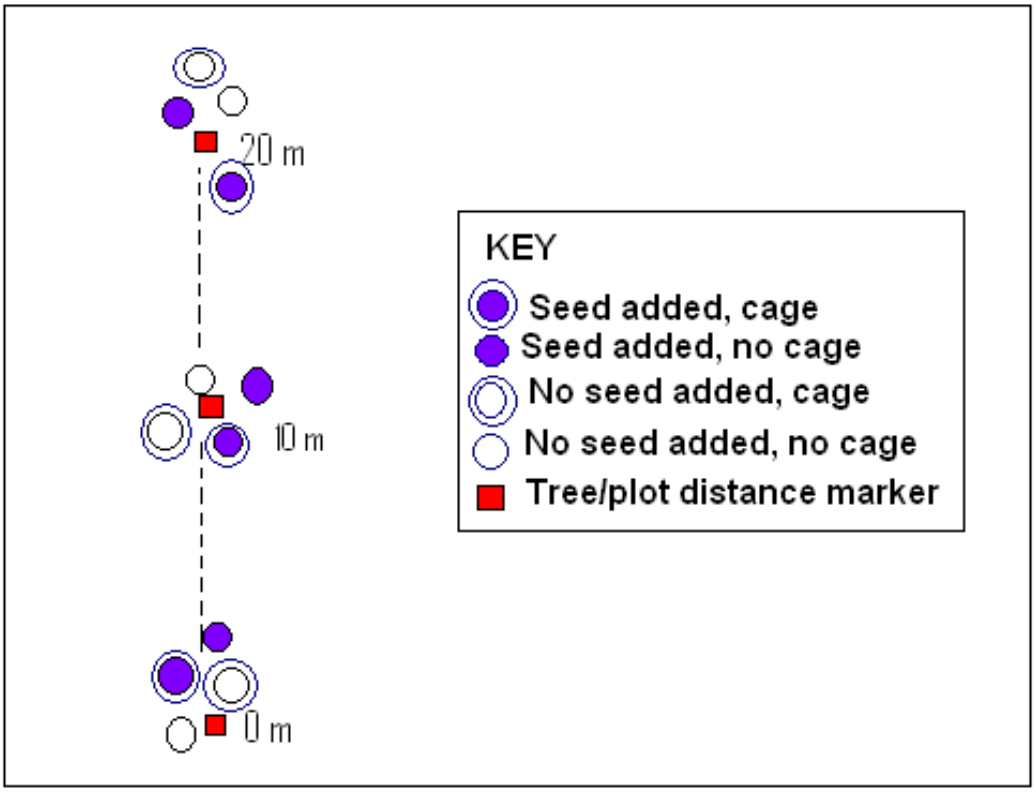
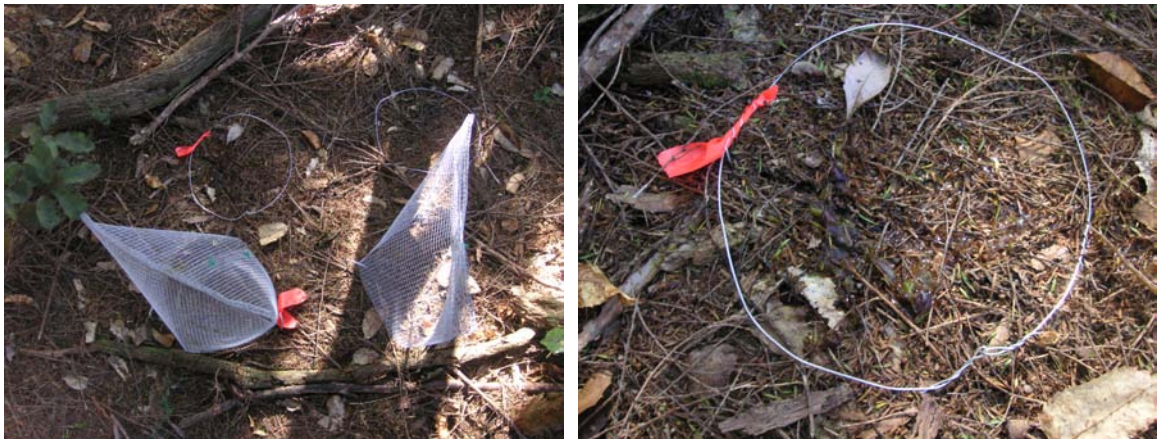


Figure 5.1: Plot set up of seed introduction experiment



a.) b.)

Figure 5.2: Cage set up at Hinewai showing; a.) The 4 replicates together and; b.) A close up of an open cage with seed added. The cage and loop with flagging tape indicate the plots with seed added.

Figure 5.3: Addition of seed slurry into a non-caged plot. Drink bottle contains water which washed any residue containing *F. excorticata* seeds onto the soil in the plot.

5.2.4 Data collection

Sites were monitored for germination over the winter, but seedlings were not found until 22 September 2009 at Hinewai. *F. excorticata* seedlings were counted twice at each site (Table 5. 2), and the highest number of the two counts at each plot was analysed.

Table 5.2: Data collection dates of germination of *F. excorticata* seedlings in seed addition experiment.

Site	First check	Second check
Hinewai	**22 Sep 09**	**24 Nov 09**
Mt Thomas	**12 Nov 09**	**18 Dec 09**
Grampians	**2 Oct 09**	**28 Nov 09**
St Arnaud	**3 Oct 09**	**29 Nov 09**

5.2.5 Statistical analysis

The experimental design required a split plot analysis in R (Version 2.10.1) (Crawley 2002) because cage and seed addition were replicated at a lower (split plot) level, but distance at the higher (plot) level. Split plots are generally presented as a series of ANOVA tables, from largest plot size and lowest replication at the top, and smallest plot size with most replication at the bottom (Crawley 2002).

Initially, the experimental design was balanced, meaning a GLM with ANOVA function would have been suitable for the split plot design; however some replicates were lost in the field, leaving an unbalanced design. ANOVA is sensitive to unbalanced data, so the model was refitted in a Linear Mixed Effects model (LME), a more robust test for data with missing values (Crawley 2002 p. 632). Mixed effects models are particularly useful when there is spatial complexity (in nested designs or split plots) (Crawley 2002), as in this experiment. The Akaike Information Criterion (AIC) (Akaike 1974) was then used in the LME results to select the most parsimonious model that best fits my data.

5.3 RESULTS

Seedlings germinated at all sites in the spring. A total of 1335 seeds that germinated were analysed. The mean number of seedlings was 2.8 across all plots. Mean number of seedlings were higher in sown plots than unsown plots, caged plots than uncaged plots, and closer to the parent tree than further away (Table 5.3). Assuming ~1300 seeds were added into each plot, a total of ~611,000 were added across all replicates, meaning 0.2% of all seeds germinated. The maximum number of seeds that germinated in one plot was 82 at a sown, caged Hinewai plot 0 m from the parent tree. All maximum number of seedlings at each distance occurred in sown caged plots at either Hinewai or St Arnaud (Table 5.3). In the sown plots 41% had zero seedlings in them, whereas 82% of the unsown plots had no seedlings. Seedlings were typically small (Figure 5.4).

Table 5.3: Mean number of seedlings germinated in each plot dependent on treatment

Test	**Treatment**	**Mean number of seedlings**	**Maximum number of seedlings**
Seed addition	sown	4.9	82
	unsown	0.7	24
Herbivore exclosure	caged	3.8	82
	uncaged	1.9	38
Distance from parent	0	4	82
tree (m)	10	2.8	55
	20	1.7	38

Figure 5.4: Photo of *F. excorticata* seedlings in a sown plot at Hinewai. Photo: Dave Kelly.

Smaller AIC on comparison of models is a relative indicator of a more accurate model fit, but adds a penalty for the number of parameters used in the model (Akaike 1974, Crawley 2002). The Bayesian information criterion (BIC) is a similar measure to AIC, but applies greater penalties for parameters used (Schwarz 1978). AIC results from split plots linear mixed effects models showed that the best model fit for my data was with all predictor variables and interaction effects (Table 5.4). BIC results showed both an interaction between caged and sown predictors, and with simple non-interaction model as being the most suited models for my data. The model with the lowest AIC (rather than BIC) is presented here, as the best AIC model shows some interesting complexities. Also, the interaction between caged and sown predictor variables was highly significant ($P < 0.001$) on the best AIC model anyway, and is presented below (Figure 5.6). Models were run using maximum likelihood (ML) rather than the default restricted maximum likelihood (REML) in order to compare mixed models with different fixed effects structures (Crawley 2002, p635).

Table 5.4: Results from split plot Linear Mixed Effects (LME) models using Maximum Likelihood (ML) and showing Akaike Information Criterion (AIC) in order to determine the most suitable model for selected data. Random effects are: “site” and “tree”. Bayesian Information Criterion (BIC) and Log Likelihood (LogLik) of the models are included in the table.

Model	**AIC**	**BIC**	**LogLik**
Pestcontrol × caged × sown × distance	3134	3213	-1547.946
Pestcontrol + caged × sown × distance	3143	3193	-1559.726
Pestcontrol × caged × sown + distance	3146	3196	-1560.864
Pestcontrol + caged × sown + distance	3153	3191	-1567.656
Pestcontrol × caged + sown × distance	3154	3196	-1567.233
Pestcontrol + caged + sown × distance	3157	3194	-1569.539
Pestcontrol + caged + sown + distance	3158	3191	-1571.062

The LME analysis of seedlings showed strong significance of the three main predictor variables, cages, sown, and distance from parent tree (Table 5.5). The coefficient column (Table 5.5) shows the direction of the effect, for instance, low pest control, open and unsown plots showed strong negative coefficients, meaning fewer seedlings in these treatments. Distance was highly significant (Table 5.5), with a decreasing number of seedlings found with increasing distance away from the parent tree.

Although interaction effects can be difficult to interpret, three interactions of particular interest which were all significant are explored in Figure 5.5 and Figure 5.6. The caged × distance interaction shows that there was a stronger decrease in seedling numbers with distance in caged plots than open plots. There were 71% fewer seedlings between caged and open plots at 0 m, 33% fewer at 10 m and actually 2% more at 20 m. The sown × distance interaction shows a steeper decline for sown than unsown plots over distance. There were 83% fewer seedlings at both 0 m and 10 m in unsown plots than sown plots, and 94% fewer at 20 m. Figure 5.6 shows the significant interaction effect of caged and sown treatments. Cages that excluded herbivores showed a much greater difference in sown plots than unsown plots, which had lower abundance of seedlings. Mean number of seedlings declined without cages by 87% in sown plots, and by 80% in unsown plots.

Table 5.5: Linear mixed-effects model fit by maximum likelihood

Random effects:

Formula: ~1 | site	Formula: ~1 | tree %in% site	
(Intercept)	(Intercept)	Residual
StdDev: 0.9583871	StdDev: 1.863823	6.302179

Fixed effects: seedlings ~ pestcontrol × caged × sown × distance

	Coefficient	Std.Error	DF	t-value	p-value
(Intercept)	15.49772	1.564131	416	9.908198	0
pestcontrollow	-10.1502	2.212881	2	-4.58685	0.0444
cagedopen	-11.5811	1.872023	416	-6.18638	0
sownunsown	-12.3652	1.890875	416	-6.53942	0
distance	-0.57586	0.102763	416	-5.6038	0
Pestcontrollow × cagedopen	8.998871	2.662083	416	3.380387	0.0008
Pestcontrollow × sownunsown	7.679192	2.675314	416	2.870389	0.0043
Cagedopen × sownunsown	9.356884	2.646099	416	3.536105	0.0005
Pestcontrollow × distance	0.412179	0.146317	416	2.817022	0.0051
Cagedopen × distance	0.600863	0.144359	416	4.162283	0
Sownunsown × distance	0.410913	0.145241	416	2.829183	0.0049
Pestcontrollow × cagedopen × sownunsown	-6.86868	3.763726	416	-1.82497	0.0687
Pestcontrollow × cagedopen × distance	-0.47703	0.206172	416	-2.31375	0.0212
Pestcontrollow × sownunsown × distance	-0.28197	0.206726	416	-1.36396	0.1733
Cagedopen × sownunsown × distance	-0.45841	0.204092	416	-2.24611	0.0252
Pestcontrollow × cagedopen × sownunsown × distance	0.376834	0.291436	416	1.293027	0.1967

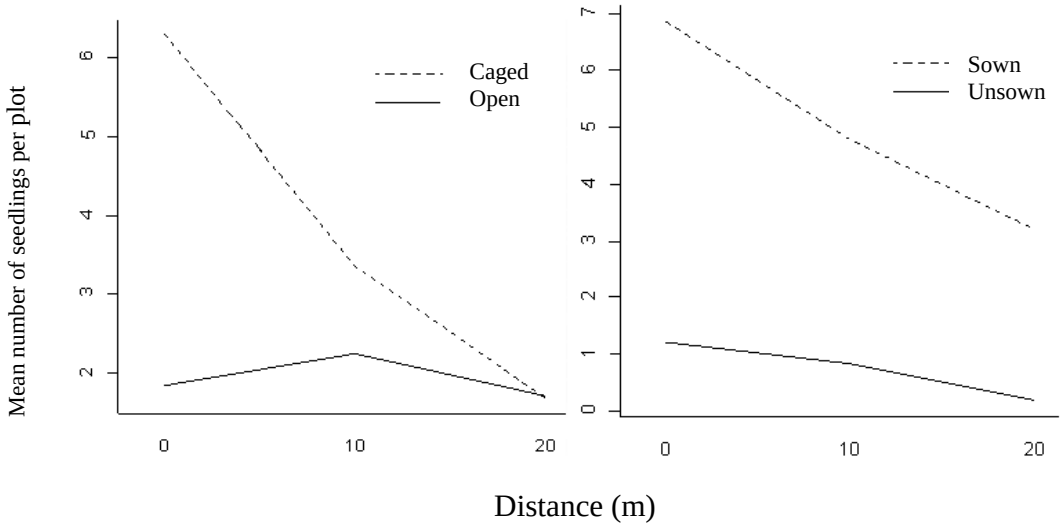


Figure 5.5: a) “Caged” × “Distance” interaction effect on seedling density of *F. excorticata*; and b) “Sown” × “Distance” interaction effect on seedling density.

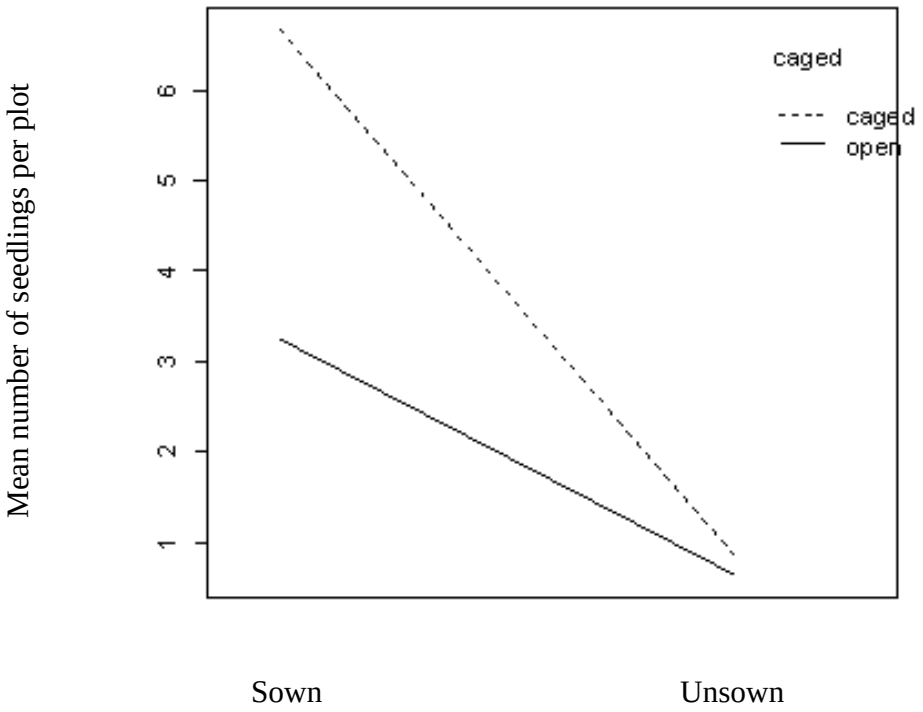


Figure 5.6: “Sown” × “Caged” interaction effect on the mean number of *F. excorticata* seedlings in plots over all distances at all sites.

5.4 DISCUSSION

5.4.1 Sowing extra seeds increases number of seedlings

As defined earlier (Chapter 1, Table 5.1), seed limitation is proven if you get an increase in population size following seed addition (Turnbull *et al.* 2000). Therefore, *F. excorticata* showed evidence of seed limitation in this experiment, due to the significantly higher abundance of seedlings (Table 5.4, $P < 0.001$) in sown plots than unsown plots. However, seed did still germinate in unsown plots (18%), which suggest that the seed bank is contributing at least some seedlings to the juvenile population.

It appears that recruitment in *F. excorticata* was limited by the availability of seeds rather than the availability of microsites (Clark *et al.* 2007), as more seeds germinated in plots with added seeds. However, microsites did also play a role in the recruitment of new seedlings, as sown plots declined in abundance of seedlings with increasing distance away from a parent tree (Figure 5.5b). Most added seeds in seed addition experiments fail to germinate (Clark *et al.* 2007), which is true in this experiment (see 5.3 – Results) because of the large number of seeds that are present in each fruit (Burrows 1995), and the number of seeds that were sown in each plot (see Chapter 5.2). Longer term monitoring of this experiment would show whether added seeds that germinate become established, as they frequently die after germination (Clark *et al.* 2007). Moles and Westoby (2002) and Turnbull *et al.* (2000) show that longer term experiments do not necessarily show an increase or decrease in the number of seedlings responding to seed addition, even though intra-specific competition may play a role in germinated seedlings in the longer term.

5.4.2 Cages and herbivore exclosure increases number of seedlings

The exclusion of herbivores to *F. excorticata* seedling plots increases the abundance of seedlings. Since *F. excorticata* is showing evidence of seed limitation, this seed predation will be producing a negative effect on the overall recruitment of new seedlings (Calvino-Cancela 2007). Slugs were observed in open plots, but not in caged plots. Established seedlings probably encounter different guilds of predators, such as possums in adult and leafy *F. excorticata* (Chapter 1.5) meaning there is a threat to survival at

any age.

Interestingly, Wilson *et al*. (2003) did not get any recruitment of new *F. excorticata* seedlings in their study of second-growth forest near Dunedin, even though *F. excorticata* is a dominant canopy species in one of their study sites, and in the understory in the other site. They did not get *F. excorticata* seedlings growing with or without exclosure cages. Presumably, this is due to a lack of suitable microsites for germination. When unsuitable microsites limit the regeneration of a species, herbivores do not matter, as they are feeding on doomed seeds or seedlings that would not become established anyway (Calvino-Cancela 2007).

5.4.3 Seedling recruitment declines with distance from parent tree

As the same quantities of seeds were added across all distances, sown plots theoretically would have produced non-significant differences between distances, however, there is a steep decline. The sown by distance interaction shows a steeper decline for sown than unsown plots over distance as habitat suitability is declining faster with distance than natural seed supply. This is reassuring for regeneration, knowing that the seed bank can naturally germinate *F. excorticata* seedlings. However the addition of seeds still dramatically increases recruitment, showing that there are a lot of dormant seeds that are not yet recruiting into the above ground population.

The distance effect is evidence of microsite limitation. As parent *F. excorticata* trees are present in the population, it is likely that seedlings could not establish at distances away from their parent trees because of unsuitable microsites for germination. Had there been suitable microsites, other older trees may have developed there already. Alternatively, seeds that germinate could suffer due to unsuitable conditions for establishment (Clark *et al*. 2007).

5.5 CONCLUSION

1) Seed limitation is evident in *F. excorticata* because of the increased recruitment of seedlings following seed addition ($P < 0.001$).
2) Herbivore limitation is affecting recruitment of *F. excorticata* seedlings as more seedlings recruited in plots with herbivore exclosure cages than open plots ($P < 0.001$).
3) Microsite limitation is proven by the significant effect of distance on sown and unsown plots ($P < 0.001$). The further you disperse away from a parent *F. excorticata* tree, the further you disperse away from suitable habitat, and the fewer seedlings there are that are able germinate.
4) The soil seed bank is contributing to regeneration of *F. excorticata* as plots with no added seed had seedlings germinate, and plots closer to the parent tree had more seedlings germinate.

Pest control is proving not only to be valuable for *F. excorticata* as a means to increase honeyeating bird numbers, and subsequent increased pollination service, but also reducing herbivory. The significant caging effect proves that herbivore pests do detrimentally influence recruitment of new *F. excorticata* seedlings; however, should *F. excorticata* become critically endangered, caging seedlings so that herbivores such as rats and slugs are unable to consume them is unrealistic.

Seed limitation is posing issues for the regeneration of *F. excorticata*, as the species is also suffering from pollination limitation. Pollen limited species are more prone to seed limitation because of reduced fruit set (Bond 1994), meaning fewer seeds in the soil seedbank. The information provided here on germination after seed addition, shows that ecologists should be alarmed by the pollination limitation of *F. excorticata* which is not producing enough viable seeds for seedling regeneration. Establishment proves to be a separate issue, which was previously discussed in Chapter 3, but could be found with longer term studies. Density dependent studies on seed limitation would be valuable, to determine whether seedling deaths are not resultant from intra-specific competition, which is a possibility with such high densities of *F. excorticata* seeds in this experiment.

Chapter 6: Discussion and synopsis

6.1 Synopsis of experiments

In this study I conducted four main experiments that aimed to answer the overall question: Is the pollen limited native New Zealand tree, *F. excorticata* seed limited? Each experiment contributed to answering this question, which is summarised in Table 6.1.

In the literature, the concept that limitations to recruitment are not mutually exclusive was reviewed in Chapter 1. Limitations can act synergistically, although they have traditionally been defined as a dichotomous paradigm: seed limitation OR establishment limitation (Poulsen *et al.* 2007). As is evident from this study, the complexities found in each experiment verify the multiple interactions that are affecting the recruitment in *F. excorticata* (Table 6.1), and that it is not simply seed limited, or microsite limited.

Surprisingly, Chapter 2 did not show that honeyeating birds were visiting *F. excorticata* flowers more often at sites with intensive pest control. Visitation was highest at the sites where *F. excorticata* was a more widespread species in high densities, which could be due to conspicuousness of the flowers and fruit, and reliance on *F. excorticata* as a prime food source. At sites where the trees were less common, birds may have other more abundant food sources that are more rewarding than *F. excorticata*. However the five minute bird counts did show higher numbers of tui and bellbird in the pest controlled sites, confirming that they are more abundant with reduced predators, but probably just foraging on other food sources if *F. excorticata* is uncommon. Pollen limitation in *F. excorticata* from lower visitation by mutualist bird partners is likely to be leading to a reduced seed output, and consequently less seed in the seed bank. This reduced seed is evident in Chapter 4, where sites with high intensity of pest control have significantly higher seed abundance in the seed bank than sites with no pest control.

F. excorticata was suffering from seed limitation because there was a highly significant increase of seedlings when seed was added to plots (Chapter 5). The interesting complexity arises when distance is factored into the experiment. With increasing

distance away from the parent, seedling density significantly decreased even in sown plots. This indicates that increasing distance away from the parent tree is likely to reduce the number of favourable microsites for *F. excorticata* germination and establishment, so microsite limitation was operating in conjunction with seed limitation (Figure 5.3b).

Seed limitation was also indicated by the widespread *F. excorticata* seed bank (Chapter 4). Normally this would ameliorate seed limitation, however because the seed bank was significantly larger in sites with pest control, pollen limitation from insufficient pollination service is presumably causing subsequent reductions in the seed set. Furthermore, female trees suffer more severe pollen limitation than hermaphrodites (Robertson *et al*. 2008), which I have found to be correlated with smaller seed banks around female trees than around hermaphrodite trees.

Herbivore limitation also operated at close proximity to the parent tree (Figure 5.3a), as seedling numbers increased in caged plots. Sown caged plots had significantly more seedlings than sown open plots, but there was little effect of herbivore exclosure when no seed was added (Figure 5.4). Seedlings were more commonly found naturally on sloped sites and sites with sparse canopy cover (Chapter 3), which suggests *F. excorticata* favours microsites with these environmental conditions. Disturbance has been proved to facilitate establishment of *F. excorticata* in the past (Burrows 1995), and for seedlings to colonise stream banks (Bartholomew 2008). Control of grazing animals at St Arnaud and Hinewai, and also proximity of the city to the Grampians may have reduced herbivory on seedlings, however Mt Thomas may encounter increased herbivore limitation because of the lack of pest control.

Seedlings were only followed for six months due to time constraints in production of this thesis. This research is essentially a snapshot of what is occurring in the populations studied, and longer term monitoring may show more evidence of establishment limitation, or, confirm results here that show seed limitation in *F. excorticata*.

The experiments performed in this study prove that *F. excorticata* was suffering from simultaneous seed, microsite and herbivore limitation, so any reductions in seed set from insufficient pollen receipt are likely to reduce the regeneration of the species. Implications are discussed below.

Table 6.1: Summary of previous chapters showing evidence of the different limitations in *F. excorticata.*

Chapter topic	**Seed limitation**	**Microsite limitation**	**Herbivore limitation**
Literature Review (summarised in Chapter 1)	Persistent seed bank (Burrows 1995) might reduce seed limitation. Widespread pollen limitation (Robertson *et al*. 2008) reduces seed supply. Seed limitation more common in early successional species (Turnbull *et al.* 2000).	*F. excorticata* typically found in disturbed seral sites, colonising sites, high light environments (Wardle 1964, Burrows 1995).	Widespread mortality caused by possums (Rose *et al.* 1993, Owen and Norton 1995, Pekalharing *et al*. 1998, Sweetapple *et al*. 2004).
Chapter 2: Site information and bird visitation	Pollen limitation may reduce seed output. Bird visitation shows interesting complexities with density and alternative food sources. Visitation not correlated with pest control, although honeyeating bird abundance in 5 minute bird counts is.		Pest control occurring at two sites, and not at other two – (no evidence from this study, but possibly higher mortality of adults at low possum control?)
Chapter 3: Natural seedling distribution		Natural seedlings were more common on well-lit and sloping sites.	Site differences in seedling density may be related to site history of ungulate control.
Chapter 4: Seed bank	Seed bank was widespread which reduces likelihood of seed limitation; BUT seed bank was smaller in sites without predator control, and decreased rapidly with distance away from parent tree (0 – 20 m). Also lower seed bank around female trees, which are more likely to be pollen limited (Robertson *et al.* 2008).		
Chapter 5: Seed addition	Highly significant effect of seed addition = seed limitation (at least at 6 months stage).	Significant decrease in seedling density in **sown** plots with increasing distance from parent tree.	Herbivore exclosure cages significantly increased seedling density, especially close to parents.

6.2 The wider picture

The functionality of mutualisms worldwide is declining due to mass global environmental change, specifically land-use change, climate change, biotic invasions, CO_2 enrichment and nitrogen deposition (Tylianakis *et al*. 2008). Species interaction networks, such as pollination and dispersal of plants, are altered by these global change drivers, which can cause ecosystem level consequences (Tylianakis *et al*. 2009). By determining the strength of these interaction networks, predictions can be made regarding the risk of plant population declines (Kelly *et al*. 2004).

Reduction in the efficiency of a pollinator service can lead to a decline in abundance and quality of plant seed set (Larson and Barrett 2000, Aizen *et al*. 2002, Ashman *et al*. 2004). Few studies actually go on to consider the dependence on seeds of pollen limited species (Ashman *et al*. 2004, Kelly *et al*. 2007). This research aimed to determine whether pollination limitation that is occurring in the New Zealand native tree *Fuchsia excorticata* was leading to seed limitation. In this research I have been able to show plant population level consequences and links from the decline in avian pollinators that *F. excorticata* relies on for mutualism services.

Table 6.2 predicts the extinction risk of a plant species given its particular life history attributes (Bond 1994). *F. excorticata* has many small seeds and a persistent seed bank, (Chapter 4, Burrows 1995) reducing its dependence on newly produced seeds (Table 6.1). Dispersal is not needed for *F. excorticata* to germinate or survive, provided it falls into a safe site for recruitment, which, according to Bond (1994) also lowers its extinction risk. However, flowers are ornithophilous and the breeding system is gynodioecious, increasing the extinction risk. *F. excorticata* flowers can be pollinated by insects, although they are apparently not the intended pollinators.

Table 1. *Plant attributes and extinction risk*

(Extinction risk is greatest when the risk of pollinator/dispersal failure, reproductive dependence on the process and demographic dependence on seeds are all high. *PS* = pollinator, *DS* = disperser specificity, *BS* = breeding system, *DD* = dispersal dependence, *SD* = population dependence on seeds.)

		dependence on process		
rank	risk of process failure (*PS*, *DS*)	pollination (*BS*)	dispersal (*DD*)	dependence on seeds (*SD*)
high 1	single species dependence	dioecious self incompatible	dispersal obligatory to cue germination, reach safe sites, evade predators	seed propagation only, lifespan (10^0–10^2 years), killed by disturbance, few large seeds, no seedbank, sparse seedlings
	specialist	self compatible		
	generalist			
low 0	wind	self pollinated apomicts	dispersal not needed for germination, recruitment or survival	vegetative propagation, lifespan (10^2–10^4 years), resprouts after disturbance, many small seeds, persistent seed bank, dense seedlings

Table 6.2: Plant attributes and extinction risk (Source: Bond 1994).

Species that lack a seed bank are likely to be more susceptible to drops in seed production (Bond 1994). It has been shown (MacDonald 1985, Burrows 1995) and further confirmed by this study that *Fuchsia excorticata* has a substantial seed bank, so should suffer less in this respect from pollen limitation. Provided seeds fall in a microsite suitable for recruitment, the seed bank is likely to contribute to regeneration.

Even though a persistent seed bank is likely to assist regeneration after disturbance, studies often overstate the importance of persistent seed banks, and understate the importance of seeds that are readily dispersed and germinate in post-disturbance sites (Dungan *et al*. 2001). Dispersal of *F. excorticata* seeds by avian dispersers is probably limiting regeneration of the species to a degree, as seeds need to drop into disturbed, high light microsites as their natural seedling distribution (as shown in Chapter 3) is typically in these environmental conditions. Also, the rapid decrease in mean density of seed bank over 20 m suggests dispersal could be functioning more effectively. Even though some plots in the seed bank (Chapter 4: particularly at Hinewai) had a large abundance of seeds at the 20 m dispersal distance, they did not have a high percentage of germination *in situ* in the seed addition experiment (Chapter 5). This indicates that germination and establishment at dispersal away from parent trees is limited by microsites, thus extending out of *F. excorticata* habitat. It is all very well having seed arrival, but a seed arriving at a site does not guarantee recruitment (Nathan and Muller-Landau 2000), as microsite

conditions may be suboptimal. A species may arrive at a site suitable for recruitment, but may also succumb to predation (Hubbell 1980).

The abundance of mature *F. excorticata* trees at Hinewai and Grampians meant that the seed bank was larger at 20 m from a parent tree than that at sites where mature fuchsia is sparse (St Arnaud and Mt Thomas). Mt Thomas has a moderate number of *F. excorticata* for a low density site, but the lack of pest control and low density of potential avian mutualist partners (Chapter 2) for pollination and dispersal means *F. excorticata* seeds are fewer in the seed bank (Chapter 4) and probably less well dispersed into potential safe sites for germination and establishment. It is also possible that the seeds at Mt Thomas are less viable due to inbreeding (Robertson *et al.* 2008).

When considering Bond's (1994) scheme (Table 6.1), it seems as if *F. excorticata* is able to cope with a weakness in one part of its evolutionary strategy (e.g. gynodioecy or ornithophily), by compensating with other features (e.g. persistent seed bank). In bet-hedging theory, individuals should avoid specialisation on a specific environmental condition in order to optimise mean fitness and reduce variance in fitness (Oloffson *et al*. 2009). Empirical evidence that bet-hedging occurs is in short supply, despite the theory being well understood (Evans *et al*. 2007), and is a possible wider context factor to consider in the complex limitations in *F. excorticata*.

6.3 Implications: Restoration and avenues for change

Global change drivers such as biotic invasions have the potential to influence ecosystem level interactions such as pollination and dispersal (Tylianakis *et al.* 2009). Focus on simple conservation of a single species can fail to recognise the wider network structure in which that species sits, and the interactions with other groups of organisms (Bascompte *et al*. 2006). The extinction of ecological interactions is what provides concern, and is easily overlooked (Janzen 1974). My study is consistent with a link between high intensity of pest control and an ensuing higher seed set in *F. excorticata* due to improved pollination services by birds (Chapter 4). This then resulted in a larger seed bank in those areas. High quality and quantity of seeds improves the potential for regeneration provided seeds fall into suitable microsites for germination.

An ecosystem level approach to restoration is likely to be a conservation strategy that becomes more prevalent in the future (McAlpine and Wotton 2009). In order to restore these pollination webs, pest control of predators of the avian mutualists of *F. excorticata* should restore bird populations to levels that would lead to the ecosystem-wide improvements that could be seen in the seed set. If *F. excorticata* is at low densities naturally, fewer seeds are likely to be made and delivered to available microsites, suggesting seed limitation. Additionally, establishment limitation is frequently stronger than seed limitation as most added seeds fail to recruit to seedling stage (Clark *et al*. 2007), so the restoration of the pollination web is likely to be more beneficial management technique to *F. excorticata* than additional input of seeds.

It is important to note not only the effect that pest control can have on a bird population, but how the increasing bird population has an ecosystem level effect on plant communities as well, as the ecosystem and community wide consequences of pollen limitation are widespread (Ashman *et al*. 2004). Kelly *et al*. (2005) sought to show this in their study to improve avian pollination of mistletoes by trapping stoats. Bellbird fledging increased from 16% to 67% and density increased by 80% with reduced stoat numbers, however there was no significant effect on mistletoe pollination or seed set. Sites with higher pest control in this study do show increased numbers of seed in the seed bank, and tui and bellbird are more common in the 5 minute counts, indirectly suggesting an improved pollination service (Chapter 4).

The Grampians site started getting frequent pest control towards the end of this study from a community group, “Birdlife on the Grampians”. It would be interesting to see whether the decline in predators from intensive trapping provided by the group leads to an increase in bellbird and tui numbers, and hence an increase in the efficiency of pollination service, and increased seed set. The Grampians provides an excellent opportunity to monitor changes before (this study) and after pest control.

The success of regeneration plans often depends on what is limiting the species, such as seed and microsite limitation (Leng *et al*. 2009), so prior knowledge of limitations of *F. excorticata* should be beneficial for regeneration plans for communities where it occurs. Similarly, this kind of early monitoring to determine the limitations to a plant species should be useful in predicting the success of a regeneration plan.

6.4 Implications: Breeding system

F. excorticata flowers and fruits for a long period of the year, (October – April), so invests a lot into a long reproductive season. Hermaphrodites are less severely pollen limited than females (Robertson *et al*. 2008), so what is the evolutionary benefit in having females if they have less nectar rewards for pollinators (Delph and Lively 1985) and if they do not produce as many seeds as hermaphrodites? This must partly be due to high disparities in pollinator visits, for if there is environmental stochasticity, any chance of fertilisation is then a chance to reproduce. A flower must frequently have unfertilised ovules after natural pollination, as seed set is often increased in hand-pollinated flowers (Ashman *et al*. 2004, Burd *et al*. 2009). This makes sense if there is stochastic disparity in mating success, which is apparently widespread in plants (Burd *et al.* 2009).

The self-compatibility of hermaphrodite flowers means there is the potential for inbreeding because of poor quality pollen receipt, rather than poor quantity (Burd *et al*. 2009), and inbreeding depression from ineffective pollination (Scofield and Schultz 2006). The big implications of gynodioecy for seed limitation in *F. excorticata* are that females are more severely pollen limited (Robertson *et al*. 2008), which is evident in the seed bank with fewer seeds around female trees (Chapter 4). The less seeds there are in the seed bank, obviously the stronger the seed limitation is likely to be.

6.5 Future research

Studies on seed limitation should follow seedlings for as long as possible. Variation in population size and habitat quality can change over time, which means that maximum carrying capacities can change as well (Munzbergova and Herben 2005). Long term experiments show more convincing evidence of limitations. Work on the New Zealand pollen limited shrub *Rhabdothamnus solandri* (Gesneriaceae**)** showed a ten-fold increase in seedling recruitment in sown plots over five years, proving strong seed limitation (D. Kelly *pers. comm.* 2010). Also, increasing number and range of seed addition experiments would be useful (Clark *et al*. 2007), in order to help determine density dependent intraspecific competition for spatial resources (Poulsen *et al*. 2007).

Seed limitation can be driven by herbivore consumer pressure (Orrock *et al*. 2008). A comparative study on an island sanctuary where bird numbers are more similar to pre-

human levels would be worthwhile, where contrast between bird visitation rates and pollination could flow onto seed set. Studies by Castro and Robertson (1997) and Anderson (2003) showed higher levels of mutualist service on islands devoid of predatory mammals where bird populations are more similar to those previously found on mainland New Zealand before the arrival of mammalian predators. Seed limitation studies extending the work by Castro and Robertson (1997) and Anderson (2003) would be useful. My study extends on the work by Robertson *et al.* (2008), and shows a link between herbivore consumer pressure (low pest control) and reduced seed set (Chapter 4).

Immediate germination was low in the field in this study (Chapter 5), yet in Bartholomew's (2008) and Burrows' (1995) lab condition experiments a high proportion of seeds germinate. This is not surprising considering seeds get washed into the soil profile and/or eaten as seeds and seedlings. However, something other than microsite conditions and/or seed supply may be influencing this success. Fungi, soil microbes, mycorrhizae and soil moisture were not considered in any of these experiments, and present a plethora of possible explanations for differences in seed germination, and provide an opportunity for collaborative studies between different biological realms.

Natural variation in spatial patterns of seeds and seedlings are linked to the spatial patterns of adults, so it can be expected that the severity of seed limitation will be dependent on the proximity to adult plants (Poulsen *et al*. 2007).

6.6 Concluding remarks

In some areas *F. excorticata* adults are suffering high mortality due to possum browse (Rose *et al*. 1993, Sweetapple *et al*. 2004), so the species has a declining reproductive population. It is also pollen limited (Robertson *et al*. 2008). However pollen limitation will not be of any consequence if *F. excorticata* is not seed limited. As *F. excorticata* has a seed bank (MacDonald 1985, Bartholomew 2008), seed limitation was thought less likely. However, *F. excorticata* did show seed, microsite, and herbivore limitation in this study. Thus, mutualism failure from reduced bird density and subsequent decline in

pollination service is threatening seedling recruitment and ultimately population size in *F. excorticata*.

This research has established that *F. excorticata* has a substantial seed bank present in sites throughout Nelson and Canterbury, but it is larger at sites where there is higher intensity of pest control. A seed bank is beneficial for reducing extinction risk of a plant species, as the species is therefore less dependent on current-season seeds falling in safe sites for recruitment. Seed addition experiments showed that *F. excorticata* was seed limited, as there was a significant increase in seedling population in sown replicates than unsown replicates. As seedlings germinated in unsown plots before current season seed had been set, there is verification that the seed bank is contributing to regeneration. However, at distances away from a parent tree less seed germinated (even when seed was added) indicating that microsite conditions became significant in recruitment.

This leads to four conclusions:

1. Sites with continuous pest control showed higher numbers of honeyeating birds in 5 minute counts, although visitation to *F. excorticata* flowers was highest at sites where density of mature *F. excorticata* trees was high.
2. *F. excorticata* seedlings naturally occurred more commonly in open disturbed sites, where light availability was high due to canopy gaps.
3. The *F. excorticata* seed bank was larger at sites with pest control, and declined significantly with increasing distance away from a parent tree.
4. Seed addition did increase the number of seeds that germinated, thus showing seed limitation in *F. excorticata.* Seedling germination was also higher in plots that had herbivore exclosure cages, and plots that were closer to the parent tree, which shows herbivore and microsite limitation with distance away from parent *F. excorticata.*

This thesis proves to managers that there is an ecosystem-wide benefit from pest control at the selected study sites, and should encourage further research into the community consequences of pollination limitation. The complex web of interactions that *F. excorticata* is an integral part of are important to understand, as an effort to conserving this highly food abundant and resource rich tree species is fundamental for conservation and restoration projects in New Zealand.

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APPENDIX 1: Map of Hinewai Reserve (scanned from Hinewai Information Brochure, H. Wilson, 2009).

Area outlined in red is where fruit were taken from for slurry and seed addition.